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SOME RESULTS OF THE FLORISSANT EXPEDITION OF 1908

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THE fourth University of Colorado Expedition to Florissant, in the summer of 1908, was only about three weeks in the field. The earlier expeditions, in 1905, 1906 and 1907, obtained a very large amount of material from the Miocene shales of this locality, and much of this still awaits study and description. A general account of Florissant appeared in the *Popular Science Monthly* for August, 1908, while briefer statements, more or less inaccurate, may be found in the current geological textbooks;[1] so it will not be necessary at this time to give a description of the place or the fossil-beds. It is pro-

[1] In Dr. W. B. Scott's valuable "Introduction to Geology," 2d ed. (1907), p. 756, it is stated that there were "very few palms." As a matter of fact, there is no reason for believing that there were any. The Rhus sp. on p. 755 is *Weinmannia phenacophylla* Ckll. In Vol. III (1906) of "Geology," by Professors Chamberlin and Salisbury, Florissant is referred to the Oligocene, following Scudder and others. It is stated that "palms are barely represented," and yews are said to occur. We do not know of any yews. It is also stated that over 700 species of Florissant insects were described by Scudder; the actual number is 569. In Handlirsch's admirable work "Die Fossilen Insekten," which would naturally be regarded as representing the best modern knowledge, numerous identifications of Tertiary insects are cited, which certainly have no value. Thus Scudder had a specimen for Florissant which looked like a Bombus: this appears in the list, without any query, as Bombus. I have seen the specimen, and it is not a bee. In Dr. Folsom's "Entomology" (1906) masses of Sialid eggs are said to occur; the eggs in question were not from Florissant, but from the Laramie beds at Crow Creek.

posed, instead, to call attention to a few of the most interesting finds of this year, especially those which can readily be illustrated by photographs. Most of the work this year was done at what we call Station 13 B, close to, and apparently of the same materials as, Station 14, from which the best things of former years have nearly all come. Superficially, 13 B seems to dip under 14, but this appears to be due to a fault; both beds belong to the older series of the locality, being covered by extensive deposits of rock and shale, the greater part of which, at 13 B, has been removed by erosion.

The shale at 13 B proved extremely uneven in quality. During the first week the results were perhaps better than in any week of former years; but the last two weeks were relatively barren, and, as we were getting a large proportion of duplicates, it was doubtful whether the work justified the expenditure. It is highly important, of course, that the Florissant beds should be further explored, and no doubt the treasures yet to be uncovered there are innumerable; but with limited resources, and great accumulations of unworked materials on hand, it has seemed better not to continue digging at the present time.

At the University of Colorado an exhibit of the Florissant fossils has been arranged. It is probably the best in existence, although the insect specimens in the Scudder collection at the Museum of Comparative Zoology, none of which are on exhibition, far exceed ours in number and variety. From the recently gathered materials, a series will be prepared for Colorado College, and also one to be sent to Dr. R. F. Scharff, for the Dublin Museum.

The members of the 1903 expedition were the same as in 1907, with the addition of Mr. Melford Smith, and, for a shorter time, Miss Gertrude Darling.

THE FISH-GENUS TRICHOPHANES

In 1872 Cope published Trichophanes, a new genus of Perciform fishes, represented by a small specimen obtained in the coal shales north of Osino, Nevada. In 1878

two other species, *T. foliarum* Cope, and *T. copei* Osborn, Scott and Speir, were added from the Florissant shales. *T. copei,* which has not been figured, is stated to differ from *T. foliarum* by its smaller scales. The genus is one of quite unusual interest, because it appears to belong to the suborder Xenarchi, an old group with peculiar anatomical characters, represented to-day by a single species, *Aphredoderus sayanus,* confined to the eastern United States. According to Jordan and Evermann, the Xenarchi are related to the Percopsidæ, of which two liv-

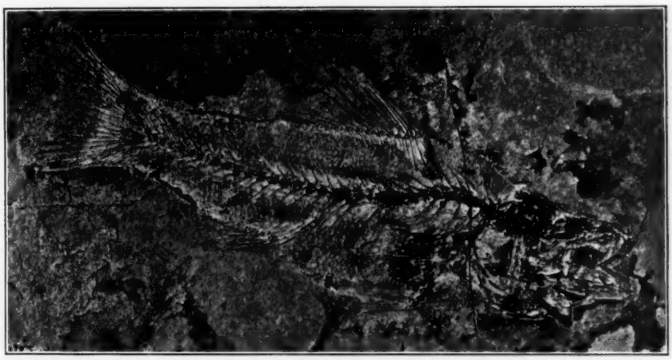

FIG. 1. *Trichophanes foliarum* Cope.

ing species are known—*Percopis guttatus* Agassiz, from the Great Lakes and surrounding regions, and *Columbia transmontana* Eigenmann, from the Columbia River. These fishes are evidently remnants of an ancient fauna, which in Tertiary times included a variety of genera and species. Agassiz, when describing Percopsis, was much impressed by its generalized features, combining characters which commonly existed together in Cretaceous fishes, but are widely separated in modern forms. "Now my new genus Percopsis is just intermediate between the Ctenoids and Cycloids; it is what an ichthyologist at present would scarcely think possible, a true intermediate type between Percoids and Salmonidæ" (Agassiz, 1850). It is remarkable that this relic of earlier days should now

have its headquarters in the area which was covered by the glacial ice; it is possible, perhaps, that it lived through the glacial period in some northern locality which was unglaciated, but cut off from the southern fauna. In this way, it might have been protected from the stress of competition, and when the great lakes were opened up, it found in them a comparatively free field—a field apparently not yet populated with anything like the maximum number of species.

FIG. 2. *Trichophanes foliarum* Cope.

Trichophanes is not precisely typical of Aphredoderidæ; it certainly seems to have some characters resembling those of the Percopsidæ, no doubt indicative of real relationship. It is readily recognized by its peculiar scales, which are ultra-ctenoid, with the marginal teeth produced into quite long bristle-like structures. According to Cope, they are "without or with very minute sculpture," but under the compound microscope they are seen to be covered with fine concentric striæ.

Cope's type of *Trichophanes foliarum* was obtained by Dr. Scudder, and consists of the anterior half of the fish only. This year my wife found at Station 13 B two prac-

tically complete specimens, herewith illustrated. These reveal many characters not visible in the type, and emphasize the Percopsis-like tendencies. In Jordan and Evermann's "Fishes of North and Middle America," plates CXXI and CXXII, are given excellent figures of Percopsis, Columbia and Aphredoderus. Our Trichophanes agrees with Aphredoderus in the thick (deep) caudal peduncle, the projecting lower jaw, and the scaly sides of the head. The dorsal fin, as in Aphredoderus, has three spines, the first very short, the third long (about 12.5 mm.), the second intermediate. The anal, as in

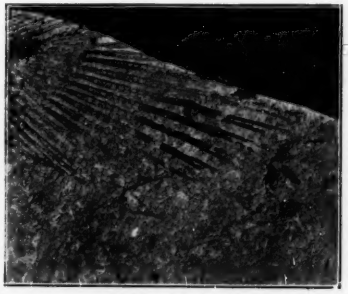

FIG. 3. Caudal fin of Amia.

Aphredoderus and Columbia, but not as in Percopsis, has two spines, one long, the other short; the longer spine is nearly straight, as in Aphredoderus. The shape of the dorsal is very much like that of Percopsis, not very like that of Aphredoderus; while the forked caudal is very unlike that of the latter genus, but rather closely resembles that of Columbia. There is no adipose fin (it is present in Percopsidæ); the ventrals are inserted about 5 mm. posterior to the bases of the pectorals, and the same distance anterior to the level of the beginning of the dorsal. In the last character the fish is nearly intermediate between Aphredoderus and the Percopsidæ.

Trichophanes should apparently be taken as typical of a family Trichophanidæ, falling in the Xenarchi, and

standing between Columbia and Aphredoderus in the serial arrangement.

Another waning group of fishes (with a single living species) found at Florissant is Amia, the bowfins. The accompanying figure shows a tail of this genus we found; much hunting failed to discover the rest of the specimen.

A PRIMITIVE DRAGONFLY

The Zygopterous dragonflies are divided into families known as Calopterygidæ and Agrionidæ. The Calopterygidæ are further divided into subfamilies, separable

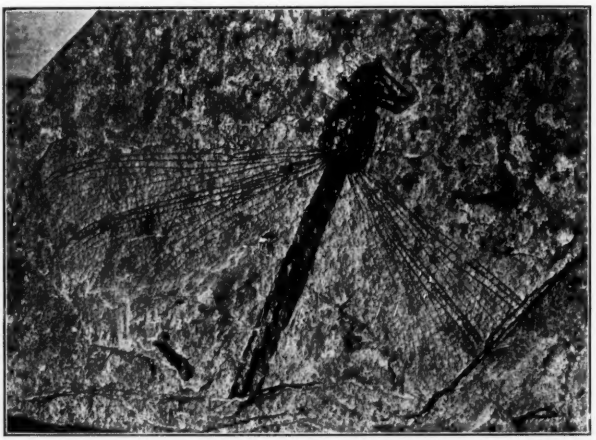

FIG. 4. *Phenacolestes parallelus* Ckll.

by the character of the costal region toward the base of the wing. In the Calopteryginæ, this area, before the nodus, is crossed by four or more veins, called antenodals; in the other subfamily, the Lestinæ, these have been reduced to two. In the family Agrionidæ, which is very abundant in the modern fauna, the reduction to two antenodals is practically universal. There is, however, an extinct subfamily, which I have called Dysagrioninæ, in which this reduction has not gone so far, and four or more antenodals remain. Of this group we know two genera, Dysagrion Scudd, from the Green River beds, and Phenacolestes Ckll. from Florissant. The latter genus,

published early in 1908 (*Bull. Amer. Mus. Nat. Hist.*) was known only from the wings. A photograph of a wing was sent to Dr. Needham, who wrote: "It is indeed a most interesting fossil, another synthetic type. . . . De Selys' Podagrion group of Agrioninæ includes the most primitive members of that subfamily, and this fossil is more primitive in several characters than any living forms." Very fortunately, a splendid specimen of *Phenacolestes parallelus* was uncovered this year by Mr. Geo. N. Rohwer. As the illustration shows, it is nearly complete, lacking, however, the apex of the abdomen. The wings are not so heavily clouded as in *P. mirandus*, the type of the genus, and there are differences in the venation. *P. parallelus* was originally described from the apical half of a wing.

Some Fossil Bees

In 1906 (*Bull. Mus. Comp. Zool.*) I described a bee's wing found at Florissant by Scudder, regarding it as the type of a new Anthophorid genus, Calyptapis. A very

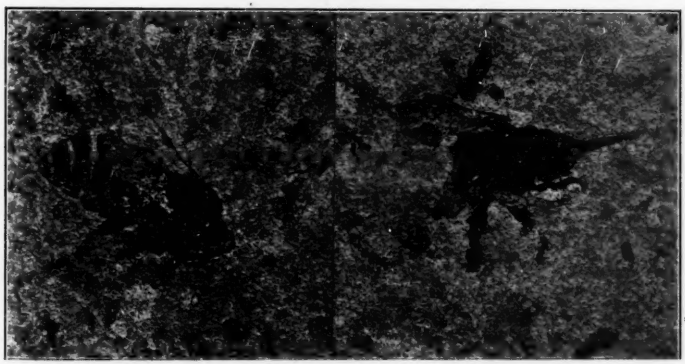

Fig. 5. Fossil bee, *Calyptapis florissantensis* Ckll.

Fig. 6. Fossil bee, *Anthophora melfordi* Ckll.

fine example, showing the body, was found this year, and from a close examination I am able to ascertain its true position. It is not an Anthophorid at all, but is a genus of Bombidæ, in other words a bumble-bee. The genus is valid, and gives the first indication of the former history

of this group in America. The insect was especially interesting to me, because I had just been studying the bees in Baltic Amber, which include various genera and species of still earlier bees related to Bombus.

Another bee of great interest was a species of Anthophora, with the mouth-parts exserted and plainly visible. Some of the amber bees show the mouth-parts very well, but it is extremely rare for those in shale to show anything of the kind. The genus Anthophora is common in Colorado to-day, but it was not previously known from the American Tertiaries.

A PROBLEMATICAL FLOWER

Last year we found, among other flowers, one which was so interesting, and so well preserved, that Dr. Arthur Hollick made it the subject of a special article in *Torreya,* September, 1907. Dr. Hollick named it *Phenanthera petalifera,* new genus and species, but was unable to place

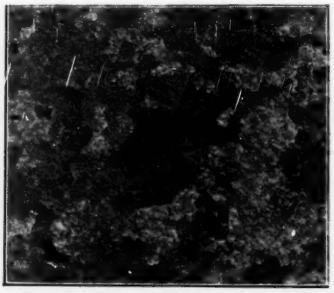

FIG. 7. Fossil flower, *Phenanthera petalifera* Hollick.

it definitely in any known family. A new specimen, figured herewith, is clearly of the same species, and on the whole confirms Dr. Hollick's description. The stamens, with long filaments and large anthers, are certainly eight in number. The supposed appendages of the calyx seem to me to be emarginate, and to resemble rather closely the small petals of certain *Ribes.* Following this clue, the large, thin "petals" may be interpreted as petaloid calyx-lobes, also as in Ribes. The short pedicels, about the length of the hypanthium, suggest that

the flowers were borne in clusters, and so in all respects they seem to agree sufficiently with Ribes, except for the insuperable difficulty of the eight stamens. The eight stamens would agree with Weinmannia, but the flower otherwise seems discordant, judging from the descriptions—I have never seen a Weinmannia flower. Both Weinmannia and Ribes are represented by leaves in the shale.

The Problem of the Proteaceæ

The Proteaceæ constitute a rather large and very characteristic family, with over 950 living species, almost confined to the Southern Hemisphere. Nearly 600 are Australian; New Caledonia has 27, New Zealand 2, Chile 7, tropical South America 36, South Africa over 250, Madagascar 2, and the mountains of tropical Africa about 5. These particulars are taken from Engler (1894), probably the numbers should now be somewhat increased. The genus Helicia, with some 25 species, is Indo-Malayan, and extends north of the equator as far as the Himalayas.

One of the most remarkable discoveries—if such it be—of paleobotany is that of the occurrence of Proteaceæ in abundance in the Tertiaries of the Northern Hemisphere. In Ettinghausen's work on the fossil flora of Häring (1853) numerous remains of leaves are figured, together with drawings of recent species of Proteaceæ. The resemblances are not merely close; it is not too much to say that the oligocene leaves look practically identical with their modern representatives. Furthermore the resemblances are not shown in one or two types only, but extend throughout a considerable series; nor are they confined to the leaves—the determinations in some instances are fortified by characteristic-looking seeds. Even the peculiar fruits of Persoonia are shown. Such evidence looked convincing enough to Ettinghausen, and *a priori,* there seemed to be no obstacle. The distribution of the Proteaceæ to-day seemed to be that of a group once world-wide, but now driven to the ends of the earth by the stress of competition. This would agree well with

the case of the marsupial mammalia, and others such as the recently elucidated one of the Chrysochloridæ, or golden moles.

On the other hand, it was pointed out that there were other leaves resembling those of the Proteaceæ. In 1870 Bentham went so far as to say, in regard to detached leaves, "I do not know of a single one which, in outline or venation, is exclusively characteristic of the order, or of any one of the genera." Quite recently Dr. Schönland (*Trans. S. African Phil. Soc.*, 1907, p. 321) has written: "The supposed identifications of southern types of plants in the Tertiary deposits of the Northern Hemisphere are considered by most eminent botanists, such as Sir Jos. Hooker, the late Mr. G. Bentham, A. Schenk, etc., as worthless. Laurent has recently tried again to prove that the Proteaceæ originated in the North, but the evidence on which he relies seems to be altogether untrustworthy." Without having seen the European fossils, it may be hazardous to attempt any contribution to this controversy; but it must be pointed out that those who regard the paleontological evidence with contempt seem to have forgotten one or two things. They have not sufficiently remembered the great antiquity of the genera of flowering plants, as shown by indisputable evidence; they have failed to consider the great lapse of time, which would permit migrations from one end of the world to the other (continuous land provided), even at the slowest rate; and more especially, they seem to have forgotten the unquestioned cases of Sequoia, Comptonia, Liquidambar, etc., in which wide-spread types have been reduced to comparatively small areas within quite recent geological times. It may also be added, that they have overlooked the analogous cases among animals, which can by no means be explained away. With all this, it must be confessed that the dicta of paleobotany are not so reliable as we could wish, and that an attitude of scepticism is often more than justified.

Lesquereux believed that he could recognize a considerable series (8 species) of Proteaceæ in the Florissant

shales. They are by no means so convincing as the European fossils; but they appear to represent an element now wanting in the North American flora, and no one has been able to show that they are *not* Proteaceous. I give figures of two of the most characteristic—*Lomatia acutiloba* and *Lomatia tripartita.* Our new material of *L. tripartita* is especially interesting as showing—what Lesquereux did not know—that it has compound leaves.

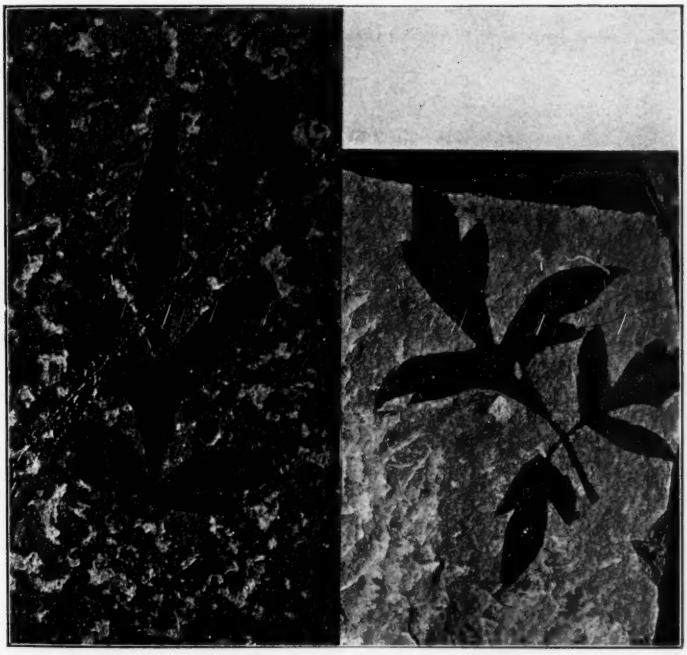

FIG. 8. *Lomatia tripartita* LX. FIG. 9. *Lomatia tripartita* LX.

These leaves are exceedingly variable, and have very much the cut of certain species of Phacelia.

This question of the Proteaceæ is one of wide importance, for it is not only a test of the accuracy of paleobotanical conclusions, but, according as it decided one way or the other, it provides or removes an argument for the former existence of great southern lands between the present continents.

A Fossil Milkweed

On the same piece of shale as the *Lomatia acutiloba,* found by Mr. S. A. Rohwer at Station 20, is the follicle of a species of milkweed. It is 54 mm. long, 14 wide in the middle, dark colored as preserved, with a longitudinal suture and without tubercles. It closely resembles the follicle of the modern *Acerates auriculata,* but is rather less tapering. It may be known as *Acerates fructifer,* n. sp. A similar follicle was described by Heer as *Acerates veterana,* and was found at Œningen and other localities.

FIG. 10. *Lomatia acutiloba* LX., and follicle of *Acerates fructifer* n. sp.

A Serviceberry

I give a figure of large serviceberry leaf, *Amelanchier typica* of Lesquereux. It is like that of the modern American *A. canadensis,* but the more cuneate base resembles that of *A. intermedia.* Other species of Amelanchier have been found at Florissant, all having a completely modern appearance, and showing that the minor groups of the genus were separated in the miocene.

A Prickly Araliaceous Plant

At Station 13 B Mr. S. A. Rohwer found a leaf with five oblong, long-stalked leaflets, as preserved light red-

dish in color, with the petiolules provided with small but very distinct recurved prickles. The leaflets are about 48 mm. long and 24 broad, with a cordate base, and the margin with broad rounded teeth or pronounced crenations, each about 2.25 mm. long. The principal lateral veins, leaving the midrib at an angle of perhaps 50°, are about seven in number on each side, and are only moderately curved. The petiolules differ greatly in length, from 26 to 5 mm., and bear a moderate number of irregularly-placed prickles, these being about 2 mm. long.

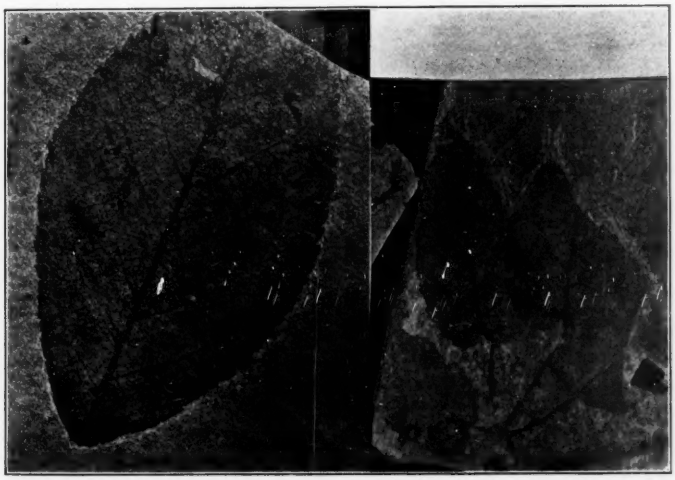

FIG. 11. Serviceberry leaf, *Amelanchier typica* LX.

FIG. 12. *Panax andrewsii* n. sp.

Mr. D. M. Andrews, of Boulder, suggested to me that this fossil was Araliaceous, and upon looking the matter up, I felt satisfied that this must be correct. I sent a photograph to Dr. N. L. Britton, who kindly replied: "There is no doubt that the photograph that you send represents some species of Araliaceæ, but I am not personally acquainted with anything quite like it. A good many of the woody Araliaceæ have prickles." From the leaf alone, the restricted genus must remain somewhat doubtful, but it may be permissible to refer the plant to *Panax*, under the name *Panax andrewsii* n. sp.

EMBRYOLOGY OF MYOSURUS MINIMUS

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THERE is a close superficial resemblance existing between Myosurus and some of the lower forms such as the pines and the Selaginellaceae. For this reason the development of Myosurus presented itself as an inviting field of research. To be sure Bessey (1898) has already given the stages in the development of the pistils. My work in so far as it repeats these early stages serves as a confirmation of his description.

The developmental stages correspond very closely to those of Ranunculus, which has been investigated by Coulter (1898). The arrangement of the pistils, however, differs from that of Ranunculus in the fact that in Myosurus the receptacle is drawn out into a long central axis around which the pistils are arranged in spiral rows. Acropetal development of the pistils is very marked, so that the axis may lengthen nearly two inches after the pistils at the base have reached maturity (Pl. I, Fig. 8). The pistils formed late in the season around the apex of the axis are not pollinated. In respect to this conical arrangement of megasporophylls and the mode of development of the megasporangia there is at least a superficial resemblance to the pines and Selaginella.

As in most microsporophylls, so here there are four sporangia. At first the stamen is a mass of undifferentiated meristem (Pl. I, Fig. 1), but soon the limits of the sporangia become visible. The meristem cells within the areas which are to become sporangia begin to degenerate, while the first hypodermal layer becomes active in division. The cells, archesporial in character, divide periclinally to produce an outer primary wall cell and an inner primary tapetal cell. The former cell divides once

or twice, producing three or four layers in the wall. The latter cuts off spore mother cells which take the place of the degenerating meristem. The tapetal layer appears to be the outer layer of spore mother cells which have sacrificed their reproductive function for the nourishment of the other cells (Pl. I, Fig. 2). In this earliest stage of tapetal differentiation, some of the tapetal cells are binucleate. A little later practically all of them become binucleate and remain so till degeneration is accomplished (Pl. I, Fig. 3). This fact, to my mind, supports the theory that tapetal cells are potentially spore mother cells. The hereditary stimulus toward further division to form microspores is strong enough in them to carry the nucleus through one division, at which point their new function usurps control and arrests further development.

The mother spores are few in number and as the anther enlarges become rounded off and separated from each other (Pl. I, Fig. 3). The usual course of development now follows. The mother cells divide simultaneously in a given sporangium to form first two and then four cells arranged either tetrahedrally or in the same plane (Pl. I, Fig. 4). The last three stages in the maturity of the microspores are shown in Figs. 5, 6 and 7. There are developed on the wall three thin spots for the extrusion of the tube. The tube nucleus, the round one, and the generative nucleus, the oval one, are always present before the pollen leaves the anther. Upon germination the generative nucleus evidently divides, for two male nuclei are found in the pollen tubes. Degeneration of the tapetum is not very marked till the pollen grains are completely formed. In the mature anther not only the tapetum but all the other cells of the wall except the epidermis and first hypodermal layer have disappeared. This hypodermal layer develops heavy bands in the cell walls for breaking the anther.

The pistil appears in its earliest stage as a small swelling on the side of the receptacle (Pl. I, Figs. 8–9).

Soon this mass of cells bends a trifle downwards, and the anlage of the sporangium appears as a swelling in the distal axil formed by the juncture of the sporophyll with the receptacle (Pl. I, Figs. 8 and 10). The end of the sporophyll now begins to bend upwards and the ovule downwards. About this time the archesporial cell appears as a single large hypodermal cell (Pl. I, Fig. 13). When the ovule has bent downwards about 90° and the seed coats have begun to appear at its sides as slight elevations, the archesporium divides rapidly to form four megaspores, arranged approximately in a longitudinal row. The first two, however, often lie more or less side by side (Pl. I, Fig. 11). In a few cases I found only three megaspores. This may have been because of tardiness in the division of one of the cells. Meanwhile a groove has been forming in the upper surface of the carpel, and as the carpel continues to bend upwards the ovule is entirely enclosed by the sides and bottom of the groove. By the time the megaspores are formed, the upper convex surface of the ovule has fused with that portion of the pistil next to it. The ovule now hangs loosely downwards in the cavity thus formed. The nucellus continues its circular movement and by the time it has bent 180° the megaspore next to the chalaza, the functional one, has enlarged, while the others have begun to degenerate. When the ovule has described an arc of 225° the functional megaspore has made its first division. Between the two nuclei a large vacuole, which continues to enlarge with the growing sac, is formed (Pl. I, Fig. 12). The cells at the sides of the sac crowd in between the sac and the epidermis. At this stage the seed coats are prominent and have three or four layers of cells. In the next stage the nucellus has advanced about 90° farther in its cycle and each nucleus of the sac has divided. With the increase in size of the sac, the cells round about it begin to degenerate. The seed coats are now as long as the nucellus (Pl. II, Fig. 14). While the nucellus is passing through the next 45° of arc all the nuclei of the

sac divide, forming eight nuclei, four at each end of the sac. The nucellus now lies parallel to the axis of the receptacle with the micropyle, which is now completely formed, directed upwards (Pl. II, Fig. 15). One nucleus from each end of the sac moves toward the center where they fuse to form the definitive endosperm nucleus (Pl. II, Fig. 17). At first this nucleus is characterized by two nucleoli (Pl. II, Fig. 19), the others having only one. Maturation is now complete, and the cell which is to become the functional egg cell may lie between or at either side of the synergids.

The pistil has now reached its final stage. It makes a slight angle with the receptacle (Pl. II, Fig. 15). The stigmatic surface is marked by long spreading cells (Pl. II, Fig. 16). The presence of chloroplasts in the cells of the style and epidermis will be noted. The ovarian cavity is almost entirely filled with the ovule. It is lined with a layer of cells which represent the original epidermal layer before enclosure took place. In surface view they are seen to be irregular cells with wavy walls (Pl. II, Fig. 24). Immediately underneath this layer is one, or in some places two, layers of long interlacing cells formed from the fibro-vascular bundle. They form a firm basket-like structure.

Already, even before the definitive endosperm nucleus is formed, the pollen tubes are found in the micropyle. About the time of the formation of the endosperm nucleus the pollen tube enters the sac (Pl. II, Figs. 18–19). The synergids at once begin to degenerate. As the tube passes into the sac the egg nucleus and the endosperm nucleus move towards each other (Pl. II, Fig. 19). The cytoplasm around the egg nucleus becomes denser and soon distinct from the other cytoplasm. It is not certain about the conduct of the generative nuclei, actual fusion stages not having been observed. Except for a few isolated observations the evidence points to the fact that the endosperm nucleus is fertilized by one of the generative nuclei and the egg nucleus by the other. The isolated

observations just mentioned were to the effect that both male nuclei were present in the sac after the endosperm nucleus had proceeded to divide. At any rate, whether the endosperm nucleus requires fertilization or not, it precedes the egg nucleus in division. This fact supports the theory that the endosperm is a portion of the gametophyte.

The first division of the egg cell is periclinal, forming two cells, the distal one of which is destined to give rise to the embryo and the other the suspensor. These two cells then divide almost simultaneously, the former transversely, lengthening the suspensor, the latter longitudinally. Either may, however, precede the other in dividing. The four-celled stage is formed by a division of the two cells in a longitudinal plane at right angles to the first plane. One or both, generally one, of the cells of the suspensor divides transversely, thus completing the suspensor which possesses three or four cells (Pl. II, Fig. 20). The proximal cell often broadens at its base. The next division of the embryo cells is at right angles to the other two planes of division and results in an eight-celled stage (Fig. 20). About this time the distal cell of the suspensor makes two longitudinal divisions at right angles to each other (Pl. II, Figs. 21–22). Numerous divisions follow in the usual manner (Figs. 21–22). In the last stages the exact arrangement of cells was hard to determine on account of the difficulty in sectioning the hardened wall of the sac. But the shape of the mature embryo with its two cotyledons and the approximate arrangement of cells are shown in Fig. 23. The embryo lies in a cavity about twice its size and so does not come into contact with the endosperm except at the base of the suspensor.

The development of the endosperm is essentially similar to that of Ranunculus. The endosperm nucleus, fertilized or not, divides successively to form several nuclei distributed throughout the cytoplasm which radiates from them as centers. The antipodal cells number-

ing three, except in one case where four were present, become distinctly separated from the rest of the cytoplasm of the sac. After the first division of the egg cell the endosperm nuclei with their cytoplasm move to the periphery of the sac, where they form a complete lining one cell in thickness. The central portion of the sac is filled with a large vacuole (Pl. II, Fig. 20). The nuclei continue their divisions till the whole sac is filled with endosperm. This occurs about the eight-celled stage of the embryo.

There is considerable variability in the time when the walls appear, but it can be safely stated that they generally appear a little after the eight-celled stage of the embryo (Pl. II, Fig. 22). However, they may occur when the sac is lined with the single layer of nuclei. The antipodals can still be seen, but are on the road to degeneration. In one case I found a peculiar condition of the endosperm. At one end of the sac were the antipodals and at the other the synergids and egg-cell. Scattered in the cytoplasm of the central portion were three large, oval, endosperm nuclei containing several large nucleoli. One of them was dividing amitotically.

The endosperm nuclei, like the pollen mother cells, always divide simultaneously. There is a rhythmical succession of activities. This rhythm is so closely followed that every nucleus is found in the same phase of mitosis at the same time. This condition is localized in individual embryo sacs and there must be, therefore, a mutual reflex stimulus among the nuclei of a given sac.

As the embryo sac proceeds in its development the cells of the nucellus degenerate (Pl. II, Fig. 14). By the time fertilization takes place all have disappeared except the original epidermal covering of the nucellus (Pl. II, Fig. 18). At this stage the seed coats which possess three or four layers of cells have grown considerably beyond the nucellus to form the micropyle. When the endosperm nuclei take a peripheral position, the original epidermal layer begins to degenerate, except a few cells

at the base of the suspensor (Pl. II, Fig. 20). The walls of the cells composing the innermost layer of the seed coats become somewhat thickened and rounded. Later the cells increase greatly in size and become very stony in texture. All the other layers except the external one, which forms a delicate membrane, disappear.

By some botanists Myosurus has been considered a low type from which the monocotyledons and dicotyledons took their origin. This view was based principally upon its external vegetative structure. If it stands on the border line between these two groups, one would expect to find in its embryology features common to both and perhaps one well-developed cotyledon and another rudimentary one. But this is not the case. The cotyledons from their first appearance clear through the period of germination are exactly equal. And, furthermore, the other features of development are typically dicotyledonous, corresponding to those of the other Ranunculaceæ. It is, however, to be regarded from its embryological and vegetative fatures as one of the lowest, if not the very lowest, of the dicotyledons.

This work was carried on in the department of botany of the University of Nebraska, under the direction of Dr. Charles E. Bessey, to whom I am indebted for his interest and assistance.

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EXPLANATION OF PLATES

Drawings were made with camera lucida. For clearness, all figures of pistils or their parts are placed on the page in the same relation to the drawing of the flower (Fig. 8) as exists in nature between the flower and the parts here represented.

PLATE I

FIG. 1. Cross section of an anther showing the region in which two of the sporangia develop. The cells are now undifferentiated. ×590.

FIG. 2. Cross section of anther showing a single microsporangium. Four mother cells surrounded by the tapetal layer. The cells of the wall are arranged radially. × 590.

" 3. Longitudinal section of anther showing the epidermis, two hypodermal layers of the wall, the tapetum composed of binucleate cells, and two mother spores. × 590.

" 4. Four tetrahedrally arranged microspores within the wall of the spore mother cell. × 590.

" 5. Three microspores just after the dissolution of the mother wall. × 590.

" 6. Still later stage of microspore with a thick wall. The nucleus has not yet divided. × 590.

" 7. Mature microspore showing the large round tube nucleus and a generative nucleus. The three thin spots in the wall are visible. × 590.

" 8. Longitudinal section through a young flower. *A*, anther. *B*, petal. *R*, receptacle. *S*, sepal. *P*, pistil. *N*, nucellus. × 35.

" 9. More highly magnified anlage of a pistil. × 365.

" 10. A little later stage showing the anlage of the ovule. × 365.

" 11. The nucellus has bent downwards 90°. The seed coat is appearing at the left, and four megaspores are present. × 365.

" 12. Two-celled stage of the embryo sac. Seed coats appear at the sides. × 365.

" 13. First appearance of archesporium. The pistil has bent upwards to enclose the nucellus. × 210.

PLATE II

FIG. 14. Four-celled stage of the embryo sac. The seed coats have grown to the end of the nucellus. The cells about the sac are degenerating. × 365.

" 15. Mature pistil and embryo sac with its three antipodals, two synergids, egg nucleus and endosperm nucleus. The dotted lines show the position of the fibero-vascular bundles. × 45.

" 16. The stigma of Fig. 15 highly magnified. × 210.

" 17. Embryo sac showing the three antipodals, the two synergids and egg nucleus, and in the center the other two nuclei fusing. × 365.

" 18. The pollen tube entering the embryo sac. The tube nucleus and two generative nuclei are present. The definitive endosperm nucleus is not yet formed. The synergids are degenerating. × 340.

" 19. Pollen tube within embryo sac. Its end, containing two generative nuclei and tube nucleus, is between the large endosperm and the smaller egg nucleus. The degenerating synergids are shown at the side. × 590.

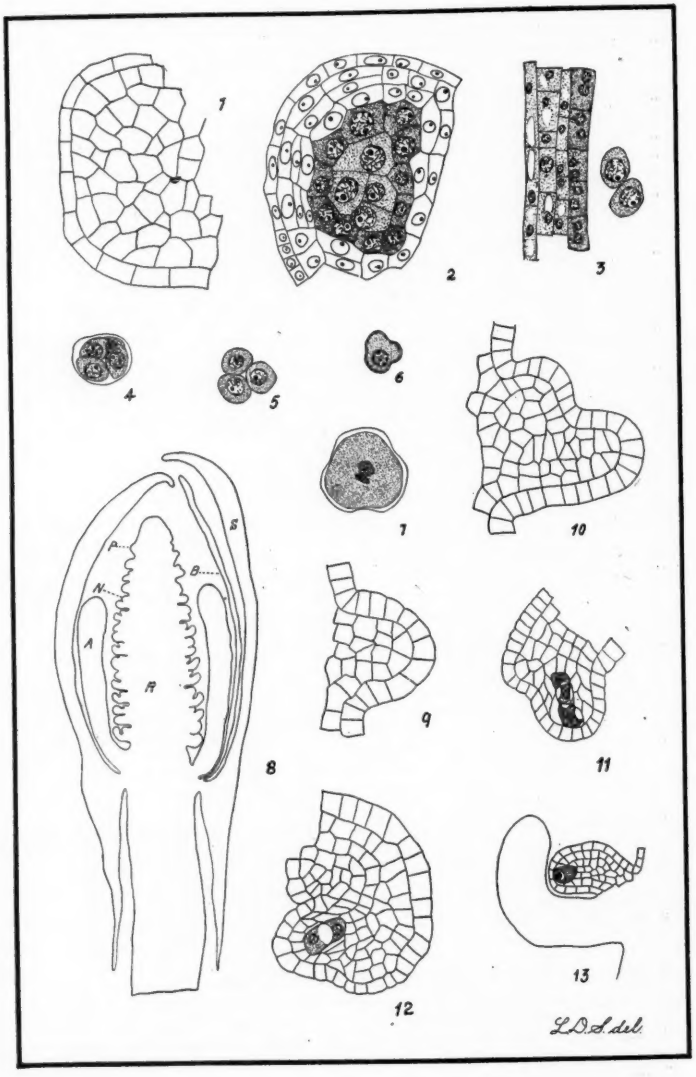
" 20. Eight-celled stage of the embryo. Three cells present in the suspensor. The endosperm nuclei are in the periphery of the sac. Three scattered nuclei of the degenerated nucellus still apparent, only five cells of the epidermal covering being left as a support for the suspensor. × 340.

" 21. A little later stage of the embryo. The distal cell of the suspensor has divided to form four cells, only two of which could be shown. × 340.

" 22. Still larger embryo. In this case there were four cells in the suspensor before the distal one divided to form four. At the left the endosperm with its cell walls is shown. × 340.

" 23. Mature embryo showing two cotyledons and three cells in the suspensor. × 365.

" 24. Surface view of epidermal cells lining the loculus. × 365.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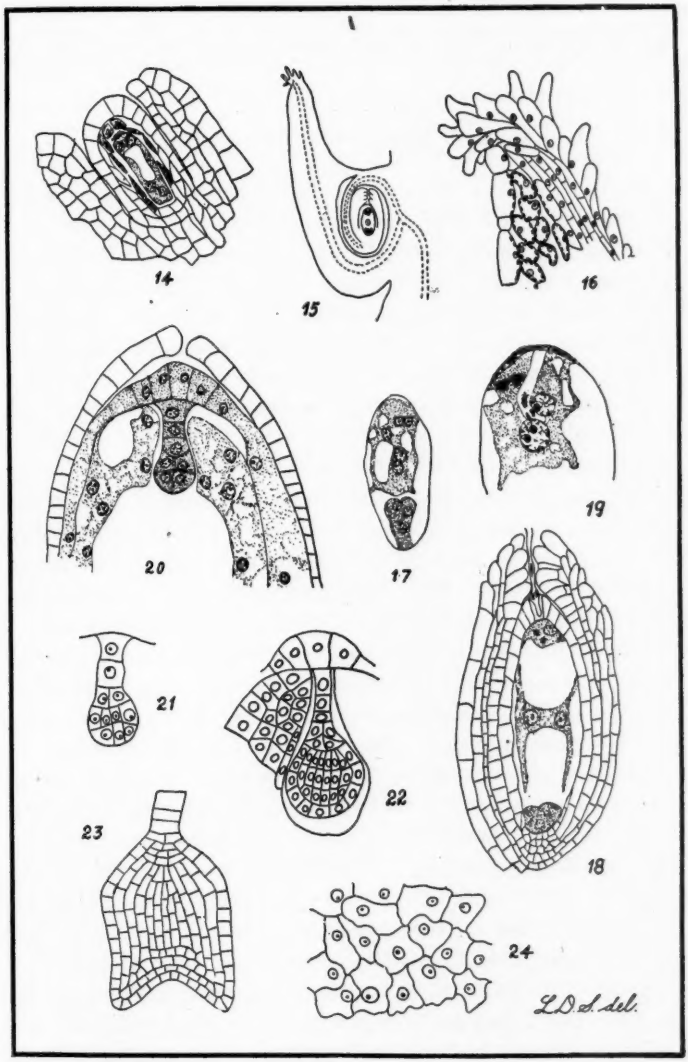
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ANOTHER ASPECT OF THE SPECIES QUESTION

DR. J. A. ALLEN

AMERICAN MUSEUM OF NATURAL HISTORY

THE AMERICAN NATURALIST for April last (Vol. XLII, No. 496, pp. 217–281) contains a report of the symposium held by the Botanical Society of America at its recent Chicago meeting on "Aspects of the Species Question." This series of eight papers should be of great interest to zoologists as well as to botanists, since it brings so strongly into relief the differences in view-point held by leading taxonomers in two widely different fields of research.

The wide divergence of views here shown in relation to the "species concept" is no less surprising than are the measures urged by some of the speakers for the reduction of "taxonomic anarchy" in botany to some degree of reasonableness. The ecologic botanist needs some method of designating the minor variations which are so important to him in his researches, but from his point of view the question "What is a species?" can be decided only by experimental research. In the meantime we may go on naming forms without essential modification of present methods. From another point of view, the naming of new forms is to be repressed with the utmost rigor, even to the establishment of a "taxonomic censorship" upon "species-making." While most of the speakers appear to agree that there are no species in the Linnean sense, and that species are merely mental concepts, like genera and the higher taxonomic groups, there is a tendency to hark back to the Linnean concept, and to accept the Linnean standard as far preferable to the minute discriminations of modern taxonomers. From other points of view there may be physiological species as well as morphological species; there may be species that

are fixed and immutable, others that yield readily to the forces of environment. That so-called species originate by different methods is evident, thanks largely to modern botanical research. The whole outcome of this symposium, as it affects nomenclature, is naturally indecisive, but contributes a few reasonable suggestions for its improvement. It is, however, a brilliant exposé of conflicting interests and conceptions.

The state of unrest, and the dissatisfaction with the *status quo* here disclosed, are not confined to the ranks of the botanists; the evils here arraigned have long agitated zoologists as well. But the organisms botanists have to deal with are so different from animals, at least the higher forms of animal life, in methods of reproduction, manner of growth, and response to environment, that the species problem in botany is a far more complex question to deal with than it is, for example, in the higher vertebrates, with which alone the writer claims familiarity.

Where to leave off naming "forms" is, after all, the main point at issue, and the next, how best to express their relationships as regards origin and degree of affinity. Utility should be, of course, the criterion in both cases, but especially in the former. How to designate the minor forms, and to what extent they may be profitably provided with names are questions that agitated zoologists apparently long before they became serious problems with botanists. Zoologists, certain of them at least, long since reached what seemed to them a satisfactory solution of the species question by recognition of the fact that "species," like genera and the higher groups, have no real existence, but are merely man-made concepts, purely arbitrary and conventional, devised for convenience in recording our knowledge of organic nature. More than thirty years ago this concept found practical recognition among American ornithologists and mammalogists, and from this hotbed of heterodoxy the infection rapidly spread until this point of view became the working basis

of their coworkers throughout the world. As early as 1884 this postulate was incoroprated in the A. O. U. Code of Nomenclature (first published in 1886), as a reason for the adoption of trinomials, in the following words:

> Recognition of the scientific fact, that a "species," so-called, is not a fixed and special creation, as long supposed, but simply a group of the same intrinsic character as that called a genus, though usually less extensive, and always of a lower taxonomic rank, has done more than any other single thing to advance the science of zoology; for the whole theory of evolution turns, as it were, upon this point.

Respecting the meaning and function of the trinomial system, it is said in the same connection:

> Trinomials are not necessarily to be used for those slightly distinct and scarcely stable forms which zoologists are in the habit of calling "varieties"; still less for sports, hybrids, artificial breeds, and the like; nor indeed to signalize some grade or degree of difference which it may be desired to note by name, but which is not deemed worthy of a specific designation. The system proceeds upon a sound scientific principle, underlying one of the most important zoological problems of the day,—no less a problem than that of the variation of animals under physical conditions of environment, and thus of the origin of species itself. The system is also intimately connected with the whole subject of the geographical distribution of animals; it being found, as a matter of experience, that the trinomial system is particularly pertinent and applicable to those geographical "subspecies," "races" or "varieties" which have become recognizable as such through their modification according to latitude, longitude, elevation, temperature, humidity, and other climatic conditions. It is obvious, therefore, that the kind or quality, not the degree or quantity, of difference of one organism from another determines its fitness to be named trinomially rather than binomially. In a word, *intergradation* is the touchstone of trinomialism.

A small amount of difference, if constant, was considered "specific," in a proper sense, while a large amount of difference, if found to lessen and disappear when specimens from contiguous faunal areas were compared, was considered as not specific.[1]

While these distinctions and principles have been found to work well in vertebrates, and have become to a

[1] Cf. A. O. U. Code of Nomenclature and Check-list of North American Birds, 1st ed., 1886, pp. 27, 31, and context.

large extent the working basis of zoologists, it is evident that they must necessarily fail to meet the needs of botanists, where the minor differentiations are of such a different character, and where so many and such diverse conditions affect differentiation within groups formerly recognized as species. Botanical nomenclature evidently must remain a makeshift, satisfactory to no one, until the ecological, physiological and experimental botanists have come to a better understanding of the causes and relations of morphological and physiological differences among closely related forms.

The introduction of trinomial nomenclature into zoology, while satisfactory for the designation of intergrading geographic forms, left still unsettled the old question of how far it is profitable to recognize in nomenclature the minor morphologic differentiations. In the cases of mammals and birds it was found necessary to reduce many so-called species to subspecies, and also to add, as material increased, many new forms under trinomial designations. These were, of course, intergrading forms, and hence arose the serious question of where to stop bestowing names upon slight morphologic variations, restricted to limited and not very clearly defined physiographic areas. As no hard and fast rule can be formulated, the treatment of such cases becomes largely a matter of temperament, experience and good judgment, in other words, the fitness of the taxonomer for his work. As is well known, the American Ornithologists Union has a permanent committee on the nomenclature and classification of North Amrican birds, whose function it is to consider all proposed changes in nomenclature and all proposed additions to the list of North American birds. This committee, consisting of seven members, is reappointed annually, and is subject to change in personnel. Its reports are published from time to time in the form of supplements to the A. O. Check-List of North American Birds, in which are given not only the accepted changes of nomenclature and the additions to the list, but also

briefly the reasons for not accepting certain of the proposed nomenclatural changes and additions. While, its authority is, of course, not final, except as regards the A. O. U. Check-List, it can throw the weight of its influence against innovations that in its judgment are detrimental to the best interests of the science. It undoubtedly acts as a powerful deterrent upon ill-considered work, and the general acceptance of its decisions by amateurs and laymen tends to the conservation, in this country at least, of a standard and uniform nomenclature for North American ornithology. It is a mild form of censorship—far less radical and drastic than that proposed by some of the botanists at their recent Chicago meeting.

As already said, the conditions in regard to the nomenclature of minor forms which confront botanists are very different from those met with in the study of terrestrial vertebrates. There is no group in mammals, birds or reptiles comparable in respect to the number, character, and association of its minor forms with Cratægus, Rubus, Aster, Sisyrinchium and numerous other botanical genera, where several recognizable morphologic forms occur in intimate geographic association. In the vertebrate classes named, the forms recognized in nomenclature that occupy the same area are always sharply separated; there is never a question of specific or even subspecific identity, except in the case of migratory birds, where several different geographic subspecies may be found associated in migration, or during the non-breeding season, in districts remote from their respective breeding ranges. Questions of identification arise, not between locally associated forms, but in reference to whether individuals from intermediate areas are referable to one or the other of the several subspecies that occur typically only in adjoining physiographic (faunal) areas. An apparent exception is afforded by the red crossbills (*Loxia curvirostra* group), where a wide range of so-called individual variation is met with, affecting the general size,

to some extent the coloration, and especially the relative size and massiveness of the bill. The extremes of variation in the latter are enormous for the size of the bird. As such individuals occur, however, more or less generally throughout the exceptionally wide (almost continental) range of the species, and are thus not characteristic of any particular locality or region, and also are everywhere associated with birds of intermediate characters, these divergent "forms" are not considered by ornithologists as entitled to nomenclatural recognition. Some years since a large-sized, large-billed, very red form was described as a subspecies under the name *Loxia curvirostra bendirei,* based on specimens from eastern Oregon. It was long held in abeyance, however, by the A. O. U. Committee, and finally rejected on the ground that no definite or distinctive geographic range could be assigned to it.

This case is cited as an illustration of the wide differences in conditions that obtain in botany and zoology. If the crossbills grew fixed to the soil like plants, and their ecology was equally open to investigation, some cause might be assigned for the development, respectively, of the large-billed and small-billed forms. At present all we know is that the common red crossbill is an exceedingly erratic species, nesting apparently with equal frequency in mid-winter or in summer, and migrating with extreme irregularity as to season and the regions visited, and characterized by an exceptionally wide range of morphologic variation. The variation in the general size of the individual, and in the size of the bill and in coloration may result from different food habits, and the lack of any sharply defined lines of morphologic separation may be due to frequent or habitual interbreeding of the different morphologic strains. The peculiar life habits and general economy of the species seem to hopelessly remove it from the field of experimental research, at least for the present.

Considering utility as the test, the trinomial system

fairly meets requirements in the case of the higher vertebrates; it seems to apply less satisfactorily in the lower animal phyla and in botany. It is admittedly preferable, however, in botany, in a large number of cases, to the binomial method, even where the variation is not geographic, since it denotes close affinity and supposed ancestry. The suggestion of Clements (*l. c.*, pp. 262–264) that, where new names are required, the third term be chosen with reference to the nature and origin of the variant, seems to offer distinct advantages.

It seems probable that the "species concept" in botany, as in zoology, can be settled only by conventional agreement; and the many interests and the diverse fields of research to be considered and harmonized, seem to relegate this desirable event to the remote future. The present diversity of views respecting the desirability and the manner of designating minor forms does not forecast a speedy agreement on even this important phase of the subject. If ever agreement is reached it obviously must come about through concert of action and mutual concessions. No radical scheme of censorship should be seriously entertained; any attempt to restrain the exercise of individual judgment will be strenuously opposed. Each man's work must stand or fall on its merits, in matters of taxonomy as in other fields of scientific research; the insistence on Latin diagnoses is a step in the direction of medieval intolerance, and apparently had its origin in personal jealousies rather than in a desire to advance the true interests of science. The ability to write in a dead language is no measure of a man's ability as a taxonomer, nor of his scientific sanity, nor of his general level-headedness as a naturalist. As said by one of the participants of the symposium:

> "What constitute sufficient morphological characters [for a species or for a minor form] must be left to the individual judgment."

The proposition to recognize by name species only and to designate minor forms—the subspecies or "races"—

numerically seems to have met with some degree of approval; which is natural, since, at first sight, it seems to present some advantages. But "*Quercus alba* race 2," or "*Draba verna,* race 104," can mean little unless the authority for the race be added as "race 2 Brown," or "race 104 Smith"; since different authors may be at work almost simultaneously upon the same group, so that race 2 or race 10 of A may not be the race thus designated by B, who at the time was ignorant of what A had done. There would be under this new method the same opportunity as at present for synonymy to play its usual rôle, the same necessity for the strict enforcement of the rule of priority. It is thus hard to see how the conditions would be improved by the adoption of a bare numeral in place of a name, which generally has some useful suggestiveness. If the authority for the race must be added to secure absolute definition, as would certainly be necessary in many instances, very little would be gained in point of brevity, and much lost in the way of aid to the memory. Should such a system be adopted and be made retroactive, chaos would hold place for an indefinite period, and the familiar verbal designations of the past, with their historic suggestiveness, would eventually share the fate of the designations of the herbalists of the past centuries. But there is probably little cause for alarm, since any serious attempt to introduce numerical designations in place of trinomials must, in all probability, demonstrate their impracticability. The proposition is more novel than practical, a protest against burdensome conditions rather than a panacea.

Another point brought out in this series of papers, though of perhaps no great importance, invites comment. It is stated (*l. c.,* p. 246):

"If I understand aright, the ornithologists, at least some of them, are willing to assert that species may differ by characters which can not be described by words [laughter]; that is to say, you will know the species when you see it, but you can not describe it in any language by which another person may recognize it. I think that this is not a

joke, but that it is really stated in earnest; because I read it in *Science*. [Laughter.] But I fancy botanists have not gone quite that far."

The author of this statement, which seems to have excited so much merriment, was simply mistaken. It would have had more basis if he had said subspecies, or "forms," instead of species, but even then would have been misleading and unfair. There are plenty of instances, among both birds and mammals, where local forms of a species are perfectly recognizable by any one as morphologically different when directly compared, through very obvious differences in coloration. But shades of color perfectly apparent to the eye are hard to characterize in language, from the fact that the color terms in current use are vague and uncertain, so that different persons may habitually describe the same tones of color in different terms, and use the same phraseology for quite different tints. It is for this reason that direct comparison of specimens is so often necessary; not that the forms themselves are so difficult to distinguish. The statement that "botanists have not gone quite that far" in describing "forms" is hardly borne out by the confession of another participant in this symposium, who says (*l. c.*, p. 240):

"The general result of these attempts to dissect nature has been embarassing because when a subsequent student takes up the group he is wholly unable to determine from any descriptions that can be written where any given individual would have been grouped by the previous author, unless he has access to the actual specimens which the previous author studied," etc.

THE ORIGIN OF THE LATERAL OF VERTEBRATES EYES

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THE steps by which the vertebrate sense organs have arisen have been traced in some measure through the evidence afforded by their embryonic growth. In this respect few systems of organs are more homogeneous. It seems to be a well established principle of embryology that all the sense organs of a developing animal shall arise from its outermost layer of cells, the ectoderm, and the fact that sense organs are the chief means by which an animal tests its environment shows that the embryonic source of these organs is not without significance, for what situation is more important for organs adapted to the reception of environmental changes than the outermost surface of the animal that possesses them. These conditions are well illustrated by most of the sense organs possessed by the vertebrates. Our organs of touch have for the most part remained where they were formed in the outermost layer of the skin. The internal ear, which in the great majority of vertebrates is a complicated sac without connections with the skin, is known to arise in individual development as a pocket from the skin secondarily cut off from that layer. Without doubt it is an excessively delicate organ of touch, for hearing and the other sensory activities of the ear seem to be dependent upon the same form of stimulus as touch, except that the kind of stimulus appropriate to the ear is much more refined than that for simple touch. Like the ear, the vertebrate organs of taste and of smell are also probably derived from the skin and in their cases they still retain the primitive connections with the mother layer, for though they are in cavities, these cavities are lined with tissue directly continuous at the mouth of the cavity

with the skin. Thus, excepting the eyes, all the more obvious vertebrate sense organs show immediate and simple relations with the external layer, the skin.

From this standpoint the lateral eyes of the vertebrate are by no means as simple as the other vertebrate sense organs. As has long been known the vertebrate retina, the essential nervous portion of the eye, does not arise directly from the external layer of the animal, but is an outgrowth from the brain. And though the brain arises by involution from the ectoderm and the retina may therefore be said to come directly from that layer, the fact that the retina does not precede the brain in its development but at best differentiates at the same time with the brain, leaves the question of the exact origin of the retina in uncertainty.

Not only is the vertebrate retina, unlike other vertebrate sense organs, not obviously connected with the external ectoderm, but it is also peculiar in the arrangement of its receptive cells, the rod- and cone-cells. In the great majority of sense organs, the receptive mechanism is made up of cells with very marked polarity in that one end of the cell is differentiated as a receiving structure and is directed toward the impinging stimulus, and the other end either tapers into a fibrous process, the nerve fiber, or is in intimate relation with nerve fibers from other cell bodies. In other words, the sense cells are differentiated in that one end serves for reception, and the other for transmission, and the cell is so placed that the receptive end is nearer the source of the stimulus than the transmitting one. In the vertebrate retina this condition is reversed. The light that enters the eye falls first upon the transmitting ends of the sense cells and only after it has passed through these cells does it reach the receptive end. The vertebrate retina is, therefore, appropriately described as an inverted sense organ. Thus the vertebrate eye departs in two important particulars from the other vertebrate sense organs: first, its sensory elements do not arise in any simple or direct way

from the outer ectoderm and, secondly, these elements are inverted in their relation to the stimulus.

As a consequence of these peculiarities of the vertebrate retina numerous theories have been proposed to account for its present condition. It must be quite clear from what has already been stated, that the chances of a simple course of development for the vertebrate retina are not great, and the first theory to be considered emphasizes this feature. This theory was first proposed by Sharp (1885); subsequently it was independently advanced by Béraneck (1890) whose views were supported by v. Kupffer (1894) and especially by Burckhardt (1901). According to this theory the primitive vertebrate retina is what we now recognize as the lens. As is well known, this organ develops as a pocket of ectoderm in the region superficial to the forming eyeball. In its early stages, as v. Kupffer pointed out, it has a striking resemblance to the beginnings of the nose and the ear and its first steps of development recall those of the eyes of many invertebrates. This primitive retina is supposed by the advocates of this theory to be metamorphosed gradually into a dioptric organ and the deeper ganglionic parts are believed to assume receptive functions and thus establish a new retina from tissue that is an outgrowth from the brain. By this process of replacement the primitive retina is converted into a lens and a secondary retina established. It will be observed that while this theory offers an explanation for the lens and for the origin of the retina from a part of the central nervous system, it does not take into account that very striking characteristic of the vertebrate retina, its inversion. Not only is this theory thus defective, but any candid reviewer must agree, I believe, with Keibel that the resemblance that the vertebrate lens has to a sense organ is only of the most superficial kind and that when one attempts to picture the steps whereby a retina is to be converted into a lens and a ganglionic mass into a retina, the difficulties come to be almost insurmountable. For these reasons this theory

has found relatively few advocates and is regarded by many as wholly untenable.

The second general theory, as to the origin of the vertebrate retina, is one which has much more in its favor and which is presented in as complete a form by Balfour (1881) as by any other. It has recently been independently advanced by Jelgersma (1906). According to this view the vertebrate retina originated on the outer surface of the ancestral vertebrate in much the way that the eyes of many invertebrates have been produced. The primitive retinas thus formed were implanted in that portion of the surface of the animal from which the central nervous system was destined to develop and when this was infolded these retinas were carried in with it, and came thus to be involved in the central organ. If the

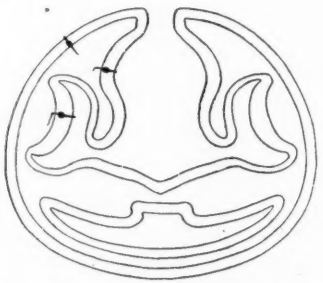

FIG. 1. Imaginary transverse section through the head of a vertebrate embryo to show the morphological relations of the surfaces of the ectoderm of the integument, the medullary tube, and the forming retina. In each of these situations a single sense cell is indicated.

morphological position of a sensory cell such as may have existed in the primitive external retina is supposed to have been retained as this organ was carried from its superficial location into the central nervous system and out again almost to the external surface, the resulting retina would be composed of inverted elements (Fig. 1). Thus this theory at once offers an explanation for the two most striking features of the vertebrate retina, namely, its formation as an apparent outgrowth from the central

nervous system and the inverted condition of its receptive cells.

The most obvious objection to this view is that the retina must be supposed to be a functional organ during this whole process of migration and inversion. But this objection, as others have already pointed out, is not serious, for if we imagine these processes to take place in animals like certain pelagic tunicates or even amphioxus, the transparency of the body would be such as to offer no hindrance whatever to the continuous action of such an organ even when in its deepest position. From this standpoint, therefore, there is no serious objection to the theory as already outlined.

The various adherents of this theory have differed considerably as to the details of its application. The general account of it already given is the particular form which was advocated by Balfour (1881) and which has since been revived by Jelgersma (1906). Balfour makes no mention of any living animal that might be taken to represent, according to this theory, a stage in the evolution of the eye. Von Kennell (1881) designated the annelids as probable ancestors and attempted to show how the external eyes of these worms could be converted into the type of eye found in the vertebrates. Jelgersma on the other hand has accepted amphioxus as an intermediate form and has based his description of the evolution of the eyes on the conditions found in this animal. These three investigators agree in believing that the vertebrate eyes have arisen from optic organs that were once on the exterior of an ancestral form. Lankester (1880) and Boveri (1904), however, do not place the origin of the eye in so remote a region but believed that it arose in the central nervous system in such a place as is now occupied by the eye of the ascidian larva (Lankester) or the numerous eyes of amphioxus (Boveri). In this way these two investigators abandon some very significant parts of the Balfour theory but in other respects they follow it very closely.

Whether we accept the annelids, or amphioxus, or still other animals as representatives of the ancestors of the vertebrates, we shall find it necessary, according to the Balfour theory, to assume some intermediate form in which the eyes are so located as to represent a condition between a primitive integumentary eye and one such as is possessed by the true vertebrates. Such a condition occurs apparently only in the minute larvæ of the ascidians and in amphioxus. As very little is known about the actual conditions in the ascidians in this respect, we shall turn our attention to the optic organs of amphioxus.

Great diversity of opinion has been expressed as to the parts of amphioxus that are sensitive to light. From recent experimental work, however, it may be taken as

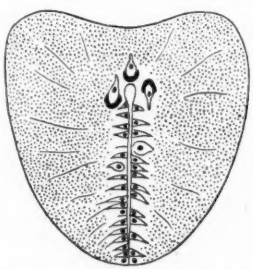

FIG. 2. Transverse section of the nerve tube of amphioxus, showing three direction eyes in place. Modified from Hesse.

fairly well established that the so-called eye-spot at the anterior end of the nerve tube and the integument of amphioxus are not sensitive to light, but that the small pigment cups described by Hesse (1898) as photo-receptive organs and found through almost the whole length of the nerve tube are the true visual organs. They lie in the substance of the nerve tube and though they have not been regarded by Hesse as in any way connected with the vertebrate eyes, they occupy a position that is very suggestive of a stage intermediate between an external eye and one such as the vertebrate now possesses.

Viewed from this standpoint the optic cups of amphioxus are not without interest. They can be seen well in any transverse section of the nerve tube of this animal (Fig. 2) provided the section is not taken from a part of the body too far toward the anterior end. In such a section the cups will be found close to the central canal. Each cup is made up of a concave pigment cell in the hollow of which is a fan-shaped cell. The expanded end of this fan-shaped cell fills the pigment cup while the handle of the fan tapers off into a nerve fiber. The whole structure, as Hesse observed, has a most striking resemblance to the simple direction eye of certain planarians, and it is difficult to resist the conclusion that amphioxus is an animal whose nerve tube is richly provided with a simple type of direction eye.

If these bodies in the nerve tube of amphioxus are direction eyes, their positions are not without significance. On examining a number of transverse sections in which they occur, it will soon be recognized that their arrangement is any thing but regular. Most of them are directed either dorsally or ventrally, but almost any position may be assumed. Though they lie near the central canal, they are not arranged in reference to it with any degree of uniformity. Some point away from it, others toward it.

The lack of uniform arrangement shown by these visual cups is of considerable importance in relation to Balfour's theory of the origin of the retina. If this theory is correct, the inversion of the retina is dependent upon a rigid orientation of the sensory cells which is supposed to have been retained absolutely from their place of origin of these cells in the external skin, through every step in their migration to their final position in the completed retina. If once in the course of this migration orientation is lost, the mechanism fails. Since amphioxus is the only animal that represents well an intermediate stage in this process, and since in amphioxus the orientation *is* lost, it seems to me that Balfour's explanation

falls to the ground. I, therefore, do not believe that the vertebrate retina is inverted because it has been inherited from an integumentary source, and I agree with Boveri that the condition in amphioxus removes all occasion for the assumption that the vertebrate retina arose on the exterior of an ancestral form and became deep-seated by being involved in the developing central nervous system. That the central organs should thus become a seat for the origin of essentially sensory mechanisms is not surprising as long as such an appropriate stimulus as light can in certain cases reach them. Even in our own bodies the respiratory reflex is maintained through the direct stimulation of the medulla by the blood that passes through it, an operation the first step of which must be equivalent to the process of sensory stimulation.

I know of no reason for assuming that the visual apparatus of amphioxus arose in any other than its present position, and I believe there is good grounds, as Boveri has pointed out, for the opinion that the visual cells of amphioxus are the homologues of the rod- and cone-cells of the vertebrates. These visual cells then probably represent the material out of which the vertebrate retina has been made. If this is true why have the eyes of vertebrates developed where they have and how does it come that their retinas are inverted?

An answer to the first of these questions can be found, I believe, in the size of the vertebrate body as compared with that of such an animal as amphioxus. In amphioxus the body is so small and thin that it is sufficiently transparent to allow light to penetrate it anywhere. Hence visual organs may be functional at any point along the length of its nerve tube. In most fishes, however, the increase of size has involved such a development of the body musculature that the posterior part of the nerve tube, the spinal cord, is completely buried in thick, almost opaque tissue. Hence visual cells would no longer be serviceable in such a region as this and they have doubtless thus been restricted to what has become the brain

region of the nerve tube. Furthermore in the brain region the development of the musculature for the gills and jaws together with the growth of the cranium as a support for this musculature must have cut off the light from below. Hence the natural growth of the body of the fish would tend to restrict the occurrence of the visual cells to the sides of the anterior end of the nerve tube, the regions from which the eyes of the vertebrates develop. It is in this partial envelopment of the nerve tube with somewhat opaque tissue that, in my opinion, has limited the eyes of vertebrates to their present positions.

An answer to the second question raised, namely, why is the vertebrate retina inverted, is found, I believe, in the structure of just such direction eyes as amphioxus possesses. The visual cell in each of these eyes has its receptive end buried in the depths of its pigment cup and its fibrous end directed outward through the open mouth of this cup. As the effective light necessarily enters the cup through its mouth, the visual cell is inverted in its relation to this stimulus. If then we imagine a retina to be formed from a great aggregation of individual direction eyes of the type found in amphioxus, it follows that the receptive elements of such a retina would be inverted. This, in my opinion, is the reason for the inversion of the receptive cells in the retina. The vertebrate retina then is fundamentally unlike the other vertebrate sense organs in that it is not directly derived from the external ectoderm, but is developed as a part of the central nervous system, and its inversion is dependent upon its origin from an aggregation of direction eyes each one of which was of necessity inverted from the beginning.

NOTES AND LITERATURE

HEREDITY

Spurious Allelomorphism: Results of Some Recent Investigations.—The original conception of a Mendelian character pair was that of two antagonistic characters, one of which dominates the other in such a way as to prevent the development of the other in individuals inheriting both characters, the *anlagen* of the two being so related to each other in the mechanism of the cell that the pair separates in the reduction division. This conception has recently been modified by leading Mendelian investigators so that now a Mendelian pair is looked upon as presence and absence of a particular Mendelian character, presence being dominant to absence. There are some apparent exceptions to this rule of dominance, but they are probably only apparent.

Some recent investigations indicate that we must still further modify our conception of pairs of hereditary characters. Bateson was the first to call attention to a case[1] which he later[2] terms spurious allelomorphism. It is a case in which two dominant characters behave in transmission as a character pair, *i. e.*, they are alternative in transmission—they can not be transmitted by the same parent to a single offspring. Perhaps, at the outset, we should broaden this conception a little so as to provide for the pairing of any two physiologically unrelated characters, whether dominant or recessive. A suitable term to designate such pairs is needed. The term *appomorphs* would answer the purpose very well were it not for the more or less arbitrary rule of philological *fashion* that hybrid words are not permitted. The first two syllables of this word are Latin, and contain the idea of apposition—the two characters are *apposed* in the reduction division. The last syllable is Greek. Possibly a hybrid word may be permitted in dealing with hybrids unless a good "pure-bred" word can be found.

The first case to which Bateson called attention was that of the erect standard and blue flower color in sweet peas.[3] These two

[1] *Science*, November 15, 1907.
[2] *Science*, May 15, 1908.
[3] *Science*, November 17, 1907.

characters form an alternative pair in the plants with which he dealt. Bateson calls attention to the interesting fact that both are characters of the wild sweet pea. Assuming that in the wild species these characters are transmitted together, we must further assume complete correlation between them; the complex pair thus being blue flowers and erect standard paired with blue flowers and erect standard. The cultivated forms have thus arisen by the loss of erect standard in one member and of the blue factor in the other, leaving the pair consisting of blue flowers on the one side and erect standard on the other. This may be clearer if we express it in formulæ. Let B = the blue flower factor, and E the erect standard. In the wild pea we have BE — BE as the pair of correlated characters, while Be — bE is the form assumed by this pair in the cultivated forms.

The next case of spurious allellomorphism was also found by Bateson,[4] while studying some extraordinary results obtained by Doncaster and Raynor in breeding certain moths (*Abraxas grossulariata* and its var. *lacticolor*). If we let G stand for the character in which the species differs from the variety, and L for the corresponding character in the variety, the results to be explained may be stated as follows:

1. ♀L × ♂G gives only ♀G and ♂G (No L).
2. ♀G × ♂L gives only ♀L and ♂G.

Furthermore, when the male used is a product of either of the above crosses, then

3. ♀G × ♂G gives ♀L, ♀G, ♂G, but no ♂L.
4. ♀L × ♂G gives ♀L, ♀G, ♂L and ♂G.

The following explanation of these phenomena is not given in Bateson's terminology, which seems to the writer to be needlessly involved, but it is based on Bateson's explanation.

Let F = the female character and f its absence.

Let G = *grossulariata* character and g its absence and assume that F and G are allelomorphic to each other.

Result No. 1 above now becomes Fg × GG = FG + GG, or female G and male G.

No. 2 becomes FG × gg = Fg + Gg, or female L and (heterozygote) male G.

No. 3. FG × Gg = FG + Fg + GG + Gg, or female G, female L, and male G.

No. 4. Fg × Gg = FG + Fg + Gg + gg, or female G, female L, male G, and male L.

[4] *Science*, May 15, 1908.

It is noteworthy that the male lacticolors produced in these experiments were the first known, all known specimens of the variety having been females. The reason for this is not far to seek. Male L's occur only when female L's mate with heterozygote males. The latter arise (from G parents) only in those matings which produce female L's (see mating No. 4 above). Heterozygote males are therefore as rare as female L's. If 1/n of the female population is L, then 1/n of the male population is heterozygote. The chance that these two shall mate is therefore $1/n \times 1/n = 1/n^2$. Hence, if only 1 female in 1,000 is L, only one male in 1,000,000 is L, which probably accounts for their having escaped the collector.

In the above case the female sex character seems to be paired with G. This is indeed a highly interesting fact, if true, and the results of Doncaster and Raynor leave little room for doubt that it is true. It now seems probable that sex is a property of a particular chromosome.[5] If this is the case, then the G character should also belong to a particular chromosome.

Bateson[5] also calls attention to what appears to be a similar case of allelomorphism between the sex character and a color element, in the case of black pigmentation of silky fowls, when crossed with Brown Leghorns or other fowls with light shanks.

I desire now to call attention to a similar case that has come under my own observation. It is well known to breeders of Barred Plymouth Rock fowls that an occasional black bird crops out in this breed, and that these blacks are invariably females. Mr. J. F. Spilman, of Wentworth, Mo., tells me that he once crossed some Black Langshan males on his Barred Rock females with the result that in the progeny all the females were black and all the males barred. I have also seen, at the Mississippi Experiment Station, some crosses between Barred Rocks and Indian Games in which part of the progeny was black, the remainder being barred. Unfortunately, in this case, no observations were made as to a possible relation between color and sex. While the data just given are insufficient to establish beyond question the following explanation, the explanation is given in the hope that it may stimulate investigation on this point. Let us suppose that the female sex character (F) is paired with the barring element (B). Let f = absence of F and b = absence of B. Then a cross between a female Barred Rock and a male Black

[5] See remarks by Bateson, *l. c.*

Langshan becomes FB × bb = Fb + Bb, or black (non-barred) females and barred males, as in J. F. Spilman's experiment. It may be plainer to some if we write the above Fb — Bf × fb — fb = Fb — fb + fB — fb.

Here F is correlated with b, and f with B; that is, in terms of the chromosome theory, the chromosome which carries F does not carry B, and *vice versa*, though these two chromosomes unite in synapsis to form a bivalent chromosome.

The origin of black females from barred parents is, under our theory, the result of mating a barred female with a heterozygote male; thus: FB × Bb = FB + *Fb* + BB + Bb.

This mating gives half of the females black, the other half and all the males being barred.

But if we mate a homozygote male barred bird with a non-barred female (carrying black color of course), we get BB × Fb = FB + Bb, both sexes being barred.

The result of this last mating has not yet been demonstrated. The same is true of the next mating, between a heterozygote barred male and a non-barred female, which should give Bb × Fb = FB + Bb + *Fb* + *bb;* that is, half of each sex black.

Some similar relation undoubtedly exists between a color element and the sex element both in geese and in ducks, for there are certain breeds of geese in which the males are all white and the females all colored; while in ducks certain breed crosses give the males all of one color and the females all of another.

Two very interesting cases of allelomorphism between two physiologically unrelated characters are found in the recently published work of Noorduijn on "Inheritance in Canary Birds."[6] The data given are not quite full enough to permit their complete elucidation, but they indicate clearly a pairing of the sex element (female) with yellow coat color, and also with a factor of the compound (from the Mendelian standpoint) eye color. There are three principal colors in canaries, namely, yellow, cinnamon (brown), and green. Since mating yellow and cinnamon always gives green birds (usually variegated, but part of the body green) we may infer that the green color arises from the combination of yellow and cinnamon, or of characters correlated with these. Noorduijn states that there are three pigments in the feathers of green canaries, namely, yellow, brown and black.

[6] C. L. W. Noorduijn, in *Arch. f. Rass-. u. Gesell.-Biol.*, April, 1908, p. 162 et seq.

In a letter to the writer he states that in a solution of potash the yellow pigment disappears very quickly, the brown somewhat slowly, while the black disappears only after a much longer interval. My interpretation of Noorduijn's results is that yellow and cinnamon color characters in canaries are probably simple Mendelian characters (unit characters), while black is due to the meeting of two Mendelian factors one of which is correlated with cinnamon and the other with yellow. The case is probably more complex than here indicated, for some of the results indicate the presence of factors in addition to those here assumd. The principal results can now be explained by assuming that C (cinnamon or brown) and Y (yellow) are independent of each other, and that the female sex element (F) is paired with Y. Noorduijn's four cases are:

I. C♂ × G (green or green variegated) females gives G♂ and C♀. This cross sometimes gives G♀'s but never C♂.

II. G♂ × C♀ gives both sexes G.

III. C♂ × Y♀ gives G♂ and C♀. Also sometimes G♀ but never C♂.

IV. Y♂ × C♀ gives both sexes G.

In the above no account is taken of variegation, which Davenport has shown to be itself a Mendelian character.[1] The Mendelian formulæ for Noorduijn's four cases now become (remembering that when C and Y occur in the same bird the color is green or green variegated).

$$\text{I. } CCyy \times CCFy = \underset{C♀}{CCFy} + \underset{G♂}{CCYy}.$$

$$\text{II. } CCYY \times CCFy = \underset{G♀}{CCFY} + \underset{G♂}{CCYy}.$$

$$\text{III. } CCyy \times ccFY = \underset{C♀}{CcFy} + \underset{G♂}{CcYy}.$$

$$\text{IV. } ccYY \times CCFy = \underset{G♀}{CcFY} + \underset{G♂}{CcYy}.$$

This does not account for occasional green females from crosses I and III, from which fact additional factors not here considered are indicated; but the formulæ indicate quite clearly that the sex element is paired with yellow coat color, or possibly with one factor of this color. This assumption is confirmed by Noorduijn's statement that yellow males tend to impress their color

[1] C. B. Davenport. Inheritance in Canaries. Carnegie Institution, 1908.

more than yellow females. According to our assumption this should be the case, since yellow males transmit yellow to all offspring, while yellow females transmit yellow only to their male offspring.

That one factor of the eye color in canaries is allelomorphic to the female sex element is also clearly indicated by Noorduijn's results. He gives only a meager portion of his experimental results on this point, so that the phenomena can not be explained here. There is enough to indicate that the case involves at least three independent Mendelian factors, one of which is correlated with yellow coat color, and hence allelomorphic to the sex element.

W. J. SPILLMAN.

HUMAN ANATOMY

Sexual and Family Variation in Centers of Ossification.—Dr. J. W. Pryor, professor of anatomy and physiology at the State University, Lexington, Kentucky, for several years has been carrying on an investigation of the ossification of the bones of the human carpus, by means of X-ray photographs. He has made a study of over 550 hands, of which 266 were those of girls and 288 those of boys. In numerous instances he has examined the hands of the same individual at different periods, and has also made a study of the ossification of the bones in children of one family compared with those of other families. In a recent article in the *Bulletin of the State University,* Lexington, Kentucky, April, 1908, he has summed up some of the conclusions arrived at in previous publications, and has brought forth new material in confirmation of his more important generalizations. He finds centers of ossification appear earlier and develop faster in the bones of the female than in those of the male, and that this difference is measurable in infancy by days, in early childhood by months, and later by years. The bones of the first child will, as a rule, ossify sooner than those of subsequent children of the same parents. There is considerable difference in the children of different families in the period when centers of ossification appear, but within a given family there is, as a rule, considerable similarity. Variation in the ossification of bones is an heritable trait. The studies of Professor Pryor enable him to give a more accurate table than has hitherto existed of the period when the centers of ossification appear in the carpal bones. The

following table is copied from his last paper (*Bulletin of the State University,* Lexington, Kentucky, April, 1908) to illustrate the rather remarkable difference in the time of the appearance of the centers of ossification in the male and female hand:

TIME OF APPEARANCE OF CENTERS OF OSSIFICATION IN THE BONES OF THE CARPUS

1. Os Magnum (capitatum)	*Female:*	between the third and sixth month.
	Male:	between the fourth and tenth month.
2. Unciform (hamatum)	*Female:*	between the fifth and tenth month.
	Male:	between the sixth and twelfth month.
3. Cuneiform (triquetrum)	*Female:*	between the second and third year.
	Male:	when about three years of age.
4. Semilunar (lunatum)	*Female:*	between the third and fourth year.
	Male:	when about four years of age.
5. Scaphoid (navicular)	*Female:*	at four years of age, or early in fifth year.
	Male:	when about five years of age.
6. Trapezoid (multangulum majus)	*Female:*	between the fourth and fifth year (preceding trapezium).
	Male:	between fifth and sixth year (preceding trapezium).
7. Trapezium (multangulum minus)	*Female:*	between fourth and fifth year (preceded by trapezoid).
	Male:	between fifth and sixth year (preceded by trapezoid).
8. Pisiform	*Female:*	between the ninth and tenth year.
	Male:	between the twelfth and thirteenth year.

C. R. B.

PLANT CYTOLOGY

Cytological Studies on Saprolegnia and Vaucheria.—These interesting and important types have been the subject of several investigations dealing with the processes of oogenesis, fertilization, etc., with conclusions at variance in a number of fundamental points. Two papers have recently appeared which should receive careful attention.

Claussen[1] reports upon oogenesis and fertilization of *Saprolegnia monoica,* contributing important evidence on points under dispute through the investigations of Trow and Davis, and pre-

[1] Claussen, P. Ueber Eientwicklung und Befruchtung bei Saprolegnia monoica. *Ber. d. Deut. Bot. Gesell.,* XXVI, p. 144, 1908.

senting a very different account and interpretation of the process of oogenesis.

There is a stage in oogenesis, before the eggs are developed, when the protoplasm forms a peripheral layer enclosing a large region free from protoplasm in the interior of the oogonium. Other authors have believed this region to be a space containing cell sap, and developed by the gathering and flowing together of vacuoles in the center of the oogonium. Claussen describes the accumulation within the oogonium of a slimy substance which he believes to be derived from the degeneration of the cytoplasm. This cytoplasmic degeneration is conceived as proceeding outward until finally the protoplasm lies as a relatively thin layer in the form of a hollow sphere under the oogonium wall. The well-known nuclear degeneration accompanies, according to Claussen, that of the cytoplasm until relatively few nuclei remain in the peripheral layer. This account of an extensive cytoplasmic degeneration to form a region filled with slime in a living active cell is not paralleled, so far as the reviewer is aware, in any cytological studies upon plants, and is likely to require more detailed study of a microchemical character before it will be accepted.

Claussen is convinced in agreement with Davis that there is only one mitosis in the oogonium and not two mitoses with chromosome reduction as reported by Trow. This is an important point, since Trow's view of chromosome reduction during oogenesis is contrary to the rule among plants that the processes of gametogenesis are unaccompanied by chromosome reduction. The species of the Saprolegniales which are sexual probably reduce the chromosome number (doubled by the fertilization of the egg) with the germination of the oospore; the apogamous species never have the double number, since the eggs develop parthenogenetically.

The account of nuclear structure, the mitosis, and their significance for the processes of oogenesis presents a point of view entirely different from both Davis and Trow. Claussen reports a central body in the resting nucleus and at each pole of the intranuclear spindle. He believes that these establish a nuclear structure with polar organization similar to that of Phyllactinia as described by Harper (see review in the July number of the NATURALIST), but on account of the small size of the nucleus the behavior of this central body was not studied in detail. Each

daughter nucleus following the mitosis is accompanied by such a central body, or centrosome, with delicate protoplasmic radiations; the greater number of these daughter nuclei degenerate. The cytoplasm begins to gather around those which survive, and such regions become the egg origins. Each egg origin has then in its interior a nucleus accompanied by a central body with radiations that extend outward in all directions through the cytoplasm. There is finally a cleavage of the cytoplasm between the egg origins and a rounding up of the protoplasm of each to form the egg.

The central body of Claussen with its radiations is very conspicuous at certain stages of oogenesis. Davis believed the structure to be analogous to the coenocentrum of the Peronosporales and to be developed in the cytoplasm without genetic relation to the nucleus. Trow described asters associated with the surviving nuclei of the oogonium and believed them to be accompanied by deeply staining material constituting a body called by him an ovocentrum. The coenocentrum of Davis corresponds to the ovocentrum and egg aster of Trow and to the central body with radiations of Claussen. The views of Claussen are very interesting and the theory is logical, but his observations on the central body are not sufficiently detailed to establish fully his conclusions. The nuclei of the Saprolegniales and Peronosporales have been studied by a number of competent observers who have failed to find a polar organization. However, these nuclei are small and the problem difficult, and further investigation may establish nuclear polarity in these groups of fungi similar to that in the Ascomycetes as determined by Harper. Should such evidence be forthcoming, the subject of nuclear structure and behavior in the Phycomycetes will take on an entirely new aspect of great significance in the explanation of the processes of gametogenesis and fertilization.

Claussen finds that the eggs of *Saprolegnia monoica* are fertilized, thus adding another form to Trow's list of sexual species, and it seems clear that fertilization occurs for a number of species in this group of fungi which is so largely apogamous. There is a single mitosis in the antheridium, with radiations around the central bodies less evident than in the oogonium. The antheridial tubes on entering the oogonium may apply themselves directly to the egg, but more frequently the ends branch and their tips become applied to several eggs. Finally

the end of such a tip opens and a sperm nucleus enters the egg, passing quickly to the female nucleus, which lies in the center and is without an evident central body. The sperm nucleus increases in size until the two fusing gamete nuclei become indistinguishable. The mitoses of oospore germination were not observed. Claussen found no bi- and tri-nucleate eggs in *Saprolegnia monoica* as were reported by Davis for an apandrous form of *Saprolegnia mixta.*

Studies on several species of Vaucheria by Heidinger[2] are reported in a lengthy paper by Heidinger on the development of their sexual organs. The investigation was conducted in the laboratory of Oltmanns and centers around the disputed point as to how the mature oogonium with its one egg comes to contain a single nucleus, when the young oogonium is multinucleate. Oltmanns described the migration or withdrawal into the main filament of all of the numerous nuclei present in the young oogonium with the exception of one, which remained to become the nucleus of the egg. Davis holds that the young oogonium is multinucleate even after the formation of the cross wall, separating it from the parent filament, and that there is a process of nuclear degeneration during which all break down with the exception of a single surviving nucleus that comes to lie in the center of the egg.

Heidinger's conclusions are in agreement with the views of Oltmanns. All of the numerous nuclei except the future egg nucleus are said to leave the developing oogonium and to pass back into the parent filament before the appearance of the cross wall which separates the oogonium from the parent filament. Heidinger finds no process of nuclear degeneration as described by Davis. The egg nucleus, which remains after the process of nuclear migration, lies at first at the tip of the oogonium and is accompanied by a centrosome-like body, with protoplasmic radiations, similar to the central body described by Claussen for the eggs of Saprolegnia; shortly before fertilization this nucleus passes to the center of the egg.

The paper gives many details of the series of events during the period of fructification and describes interesting culture methods. The cytological account is, however, open to criticism. The fixation was in ½–1 per cent. chrom-acetic acid, a very

[2] Heidinger, W. Die Entwicklung der Sexualorgane bei Vaucheria. *Ber. d. Deut. Bot. Gesell.*, XXVI, p. 313, 1908.

strong fluid for such delicate algæ, and there was evidently much shrinkage of the material, as shown in the outlines of the text figures. These latter are not satisfactory, considering the importance of the details which are discussed, and in the opinion of the reviewer are not convincing. There are some fundamental principles concerned in the discussion between Oltmanns and Davis which will require more thorough investigation before final conclusions are likely to be reached. The most important of these concern the history of the developing oogonium after the multinucleate stage, and the factors that lead to the selection of the nucleus which comes to preside over the egg.

BRADLEY M. DAVIS.

HOLOTHURIANS

Holothurioidea.[1]—Under the above title Östergren has made a noteworthy contribution to the literature concerning the Holothurioidea. Based upon years of special study of the group, he concludes that in order to estimate the value of an organ in taxonomy and phylogeny, the function of the organ must be completely understood.

Ostergren first discusses respiration, particularly in connection with the enteron as respiratory organ. By means of their dilator muscles, sometimes the œsophagus, but most often the cloaca, functions as a pump to force the water into other parts of the enteron, or into especially developed extensions of the same. The primitive condition is found in the Synaptidæ.

In most of the Elasipoda respiratory trees are lacking, and yet the cloaca is provided with dilators, and doubtless functions as a pump to force water into the enteron. As Ludwig (1889–92) points out, in various members of the Elpidiidæ and Psychropotidæ, a simple unpaired evagination appears as a "rudimentary gill," or water-lung. From such a beginning comes the single, or double, stemmed respiratory trees. Since it is possible to have within a natural genus certain species without water-lungs, others with them rudimentary, and still others with well-developed respiratory trees, Östergren maintains that the presence, or absence, of these organs is of no particular importance in taxonomy.

[1] Östergren, Hjalmar. Zur Phylogenie und Systematik der Seewalzen. Särtryck ur Zoologiska Studier tillägnade Professor T. Tullberg. Upsala. October 12, 1907.

The pedicels have not the same importance for locomotion in sea-cucumbers as in sea-urchins and star-fishes. The sea-cucumber moves by worm-like contractions of the parts of the body. The pedicels on the part temporarily at rest either suck hold of the solid bottom or bore into the slime, and thus serve to give a firm basis from which the other parts of the body may be extended. Östergren (1897) proves that the anchor-like spicules of the Synaptidæ are locomotor. Even in the pedate holothurians, the spicules help to make a firm anchorage for the resting part of the body while the moving part is bent away from the bottom and thus the rough points made by the spicules do not hinder the forward movement. Some sea-cucumbers, like the remarkable Pelagothuria, swim, and in them the pedicels are small and weak.

On the other hand, the Dendrochirotæ, which remain for a long time in one spot, have well-developed pedicels so that they can suck fast to rocks, or algæ, or on soft bottom, burrow into the slime and by means of their suckers ballast themselves with stones and fragments of shells. The pedicels often gather weeds and shells which form a protective mask. In holothurians without pedicels, the spicules serve for this protective function. In very different groups spicules of the same form, albeit actually fundamentally different, may be developed without indicating any natural relationship of the groups. Such, for instance, are the anchors of the Synaptidæ, and the Molpadiidæ. The branching of the calcareous rods is always in a manner best adapted to form the spicule with economy of material.

While admitting that pedicels and tentacles are homologous as external appendages of the ambulacral system, Östergren claims that they are distinctly different, with no connecting links between, and therefore, like Perrier (1902), declines to follow Ludwig's (1889–92) characterization of the Synaptidæ as having tentacle-feet, and no body-feet. On the other hand, he does not follow Perrier in classifying the Molpadiidæ as apodous, but considers the anal papillæ as reduced pedicels which, like similar appendages in the Aspidochirotæ and Dendrochirotæ, have evolved as tactile organs.

Ludwig (1891) proves for one of the Dendrochirotæ, *Cucumaria planci,* and the present writer has shown (Edwards, 1889, 1905) for one of the Aspidochirotæ, *Holothuria floridana,* that the tentacles develop from the radial canals in the same manner

as the pedicels. Furthermore, in *Holothuria floridana* at first the tentacles are provided with terminal suckers and these organs, like the primitive pedicels, are used for locomotion, while in feeding, as in the adult, they push food into the mouth. Admitting that the distal anal papillæ are modified pedicels, I think it is reasonable to consider the proximal oral tentacles as pedicels, only much more modified in the adult, for their special functions.

Östergren imagines the primitive form, or "Stammholothurie," as having had a soft body-wall containing spicules, and with five simple radial muscle bands, interrupting the transverse sheet of muscle. It moved by contractions of the body, and ate slime. The stone-canal was simple and opened on the outside of the skin. There were many pedicels and either ten or twenty tentacles without ampullæ. The calcareous ring had five radialia and perhaps five interradialia. The enteron was in three loops, the third in the right ventral inter-radius. The blood system did not expand into a *rete mirabile*. The posterior end of the enteron developed as a respiratory cloaca but respiratory trees were not present. There were no auditory vesicles. Östergren's primitive form was most nearly related to the present Elasipoda, and from it he shows how the five chief divisions of the class Holothurioidea may have evolved. Östergren employs as the names of these orders, Elasipoda, Aspidochirota, Dendrochirota, Molpadonia and Apoda (Synaptidæ, Chiridotidæ and Myriotrochidæ), and then concludes with a general description of the chief characters of each order.

CHARLES L. EDWARDS.

THE ENTEROPNEUSTA

Recent Literature on the Enteropneusta. 1. *Systematic.*—Spengel has lately given the classification of the Enteropneusta a thorough overhauling.[1] This accepted imperator in the knowledge of the group recognized at the time 31 species, 9 genera and 3 families. Since then 14 species and one genus have been added. Nearly all the new ones have come from the Pacific and Indian Oceans, these two enormous reservoirs of unknown organisms, the exploration of which has but recently begun in earnest. R. C. Punnett's report, The Enteropneusta in the "Fauna and Geography of the Maldive and Laccadive Archi-

[1] Die Benennung der Enteropneusten-Gattungen. *Zoolog. Jahrb.*, 15 Bd., pp. 209–218, 1901.

pelagoes," Vol. II, Part 2, pp. 631–680, 1903, stands first in point of numbers of new forms, 5 species and 1 genus being added in this, all but one coming from the island groups mentioned in the title. The exception, the type of the new genus Willeyia, comes from Zanzibar. Besides the 5 full-fledged new species recognized by Punnett, the 6 varieties of an old species *Ptychodera flava* are interesting. These are based on a statistical study of the 222 specimens in the collections. This is the first effort made to treat any of the Enteropneusta statistically, and is noteworthy on that account if for no other. The author's attitude toward the subject seems practical and sane. He remarks: "I am not here concerned with the question of the statistical method as a criterion of species and varieties. My point is that in the group of animals collectively designated *Pt. flava* there are to be found different positions of organic stability, and in giving to these 'a local habitation and a name' there is no thought of distinguishing by statistical methods between the terms *race, variety* and *species.*" The only question would be as to the sufficiency in number of specimens examined and the structural features considered to justify all these subdivisions in this particular animal, and the question is to be answered only by further examination of more material.

The next largest numerical contribution is from the Siboga Expedition (Studien über die Enteropneusten der Siboga-expedition, Monographie XXVI, pp. 1–126, 1907, by J. W. Spengel). Three fully accredited species are here described. Worthy of note, perhaps of approval, is Spengel's practise, which is specially illustrated in this report, when dealing with certain forms which he finds to differ somewhat from any already recorded species, but yet not sufficiently to warrant giving them full specific rank on the basis of the small evidence at hand. To these he attaches a "provisional" specific name. Three such names are used in this report. They usually designate specimens from a particular geographic locality.

Spengel appears to be ever dubious about the specific identity of specimens of Enteropneusta occurring in widely separated places. Thus in his "Neue Beiträge zur Kenntniss der Enteropneusten," I and II (*Zoolog. Jahrb.*, 1903 and 1904), he examines in great detail specimens of *Ptychodera flava* Eschsch. from Laysan, and concludes that they differ sufficiently from those described by Willey from New Caledonia, to deserve being

treated provisionally, as distinct. Similarly he examines (Beitrag II) specimens from Funafuti and concludes that these are also recognizably different from those from the type locality. We consequently have as "provisional" designations *Ptychodera fl. caledoniensis, Pt. fl. laysanica,* and *Pt. fl. funafutica.* The author points out that while Funafuti (8° 30′ S.) lies between New Caledonia (20° S.) and Laysan (26° N.), *Pt. fl. funafutica* is not intermediate in structure between the other two forms.

One might, perhaps, question the utility of speaking of such designations as provisional when as a matter of fact no zoological name whatever can be confidently claimed to be final. In the reviewer's opinion there is, nevertheless, real merit in Spengel's practise. It seems to him that proof of the tendency of plant and animal kinds to break up into more kinds as soon as ready means of intercommunication is prevented, is so strong that the systematist is generally bound to suspect that specimens from widely separated localities (at least in many groups) are different until they are shown not to be so. This provisional naming might be looked upon as a recognition of this principle.

Another Pacific species is from Japan (On a new Enteropneust from Misaki, Balanoglossus misakiensis, n. sp.)[2] and another Indian Ocean one from the coast of India (Enteropneusta from Madras).[3]

Hardly less notable than the new species from the least explored parts of the sea is the bringing to light of new ones in the best explored parts. Spengel[4] describes a species of Glossobalanus from the Bay of Naples. The author well remarks that it is "sicher aufallend" that a new species represented by a single specimen should stand accredited to shallow water in the immediate vicinity of the Naples Zoological Station.

2. *Development.*—What must be counted as the most important contribution to Enteropneust development that has appeared since Bateson's series of papers, 1884–1886, has just been published by Dr. B. M. Davis (The Early Life-history of *Dolichoglossus pusillus* Ritter.[5] Davis had shown four years earlier that this California species develops without passing through a tornaria stage. *Dolichoglossus* (*Balanoglossus*) *Kowalevskii* of the Atlantic Coast of the United States, the species studied by

[2] *Annot. Zool. japon.*, Vol. 4, 1902, pp. 77–84.
[3] *Quart. Journ. Micro. Sci.*, Vol. 47, 1903, pp. 123–131.
[4] Neue Beiträge III, *Zoolog. Jahrb.*, 20 Bd., 1904, pp. 315–362.
[5] *Univ. of California Publications in Zoology*, Vol. 4, 1908, pp. 187–228.

Bateson, develops directly also, it is hardly necessary to mention. Since the two species are much alike in most other respects as well, the desirability of examining the development of the Pacific species was obvious. The report before us is confessedly incomplete so far as the entire developmental history is concerned. In some of the phases treated it is, however, measurably full and apparently conclusive. The point of most importance perhaps as developmental problems are now estimated, pertains to the origin of the body cavities. Bateson seemed to find these to arise as five diverticula from the archenteron, viz., one anterior which produces the cavity of the pre-oral lobe, or in the final state the proboscis, a pair immediately behind this producing the cavities of the collar region of the adult, and behind these another pair which produces the cavities of the rest of the animal, *i. e.*, of the thoracic and abdominal portions.

Davis finds a radically different course of things. In the embryo studied by him a single anterior pouch arises as in *D. Kowalevskii,* but instead of the two pairs coming directly from the archenteron, the one anterior pouch sends back lateral pockets between the ectoderm and endoderm, and from these there is constricted off first a pair of cavities which correspond to the future collar, and then in turn from the posterior end of this collar pair, a second pair, presumably representing the future cavities of the thoracic-abdominal region of the adult, is cut off. Since Davis's results rest upon the examination of a large number of embryos (about one hundred and fifty series of sections, he tells us), preserved in a variety of ways and cut in various directions, it seems they must be accepted, and so the conclusion reached that either Bateson's interpretation of his sections was seriously erroneous, or that these two species so closely alike in most respects are unlike in this supposedly fundamental point. Davis strongly inclines to the first view and presents cogent reasons for his inclination based on a critical study of Bateson's text and figures.

The bearing of this finding on the problem of the relationship between Balanoglossus and Amphioxus is clear. The supposed similarity of origin of the body cavities has been taken as a leading proof of genetic kinship between the two animals. Davis does not fail to point out that his observations justify the doubts of the correctness of Bateson's conclusions entertained by both Spengel and Morgan and drawn from their studies of tornaria.

While Davis's work greatly weakens one of the strong supports of blood relationship between these two groups, it does not leave this weakening wholly uncompensated. It seems to find a number of striking resemblances between the egg cleavage of this particular enteropneust and that of Amphioxus. But this part of the study is less full and the significance of resemblance in these earlier developmental stages is more problematic. For the character of the correspondences here the reader must be referred to the paper itself.

3. *Ecology and Physiology.*—Ritter and Davis[6] have studied quite fully the movements of a tornaria of the California coast from near the beginning to the end of its pelagic career. A number of interesting facts pertaining to the character of the swimming movements, the correlation of these with its specific gravity, and this again with its structure are brought out.

Davis (paper on the development of *Dolichoglossus pusillus* already referred to) discusses some points on the distribution and migration of this species as dependent upon the movements of the animal during its larval period, and upon tidal action. Davis finds that the breeding time of *D. pusillus* in San Diego and Mission Bays is January and February, and that the fertilized eggs can be obtained from the burrows of the animals at low tide without great difficulty. Particularly noteworthy is the fact that in spite of the absence of a true tornaria, the young animal still does considerable swimming, and that this follows rather closely the general scheme previously found by Ritter and Davis to characterize the swimming of the tornaria of another species above alluded to.

Ritter[7] has studied the movements of the adult *Dolichoglossus pusillus* and a California species of *Balanoglossus* with the special view of gaining a better understanding of the action of the proboscis and skeletal musculatures and the relation of these to the skeleton. The results make it probable that the nuchal skeleton together with the so-called notochord serves not merely as a support for the isthmus, or neck, but also as an axis upon which the muscles of locomotion act, in part at least.

4. *Anatomy.*—The classification of the Enteropneusta is based

[6] Studies on the Ecology, Morphology, and Speciology of the Young of Some Enteropneusta of Western North America. *Univ. of Calif. Publications, Zoology,* Vol. I, 1904, pp. 171–210.

[7] The Movements of the Enteropneusta and the Mechanism by which they are accomplished. *Biolog. Bull.,* Vol. III, pp. 255–261.

on a thoroughgoing examination of everything in the make-up of the animals, thanks particularly to the standard set by Spengel's splendid monograph of 1893. From this circumstance it follows that anatomical studies on the adults of either old or new species are not likely to yield greatly important new facts. A few points of considerable general interest, however, come from recent work.

The superficial, presumably secondary, metamerism of portions of the body in several species has attracted the attention of most observers. Willey and Spengel have given it special consideration. In no known species is this more strikingly seen, perhaps, than in the Neapolitan one lately described by Spengel. The prominence and regularity of the bilaterally arranged crosswelts or ridges on the ventral side of the genital region as figured by him, are remarkable indeed. It is not likely that these structures have any great significance either phylogenetic or physiological. They are probably in the main growth characters and are interesting on just this account.

In his extensive studies on the excretory organs of annelids and amphioxus some years ago, E. S. Goodrich predicted that a peculiar type of cells observed in these animals and called by him Solenocytes, would on special search be found in the Enteropneusta. Spengel has given attention to this point, with negative results so far. (Beitrag III.)

References may here be made to Spengel's tilts with Arthur Willey on the latter's speculations as to the vertebrate homologies of various Enteropneust organs. For example, Spengel examines with his accustomed thoroughness the dorsal nerve roots of the collar region in several species and treats with quite pungent sarcasm Willey's contention that in these we have the homologues of the vertebrate epiphysis. A fragment of this particular tilt is worth repeating as literature, though it may be questioned whether Willey ever took himself seriously enough in much of his theorizing on these matters to warrant giving his utterances much time under the aegis of real science. "An epiphyseal structure," Willey is quoted as saying, "like an enteropneustic root, can be transformed into an epiphyseal structure like a pineal eye by losing its primary function . . . passing through a condition of pigmentose degeneration . . . and then being rejuvenated by the acquisition of a new function." Then Spengel himself, "wo in aller Welt giebt es eine

Stütze für eine solche Annahme, dass ein pigmentoser Degeneration anheimgefallenes Organ einer Verjüngung durch Erwerbung einer neuen Funktion fähig wäre . . . ???—und dann schliesst gar der Satz, the agens of rejuvenescence being some form of natural selection! . . . heisst das etwa nicht, den Spöttern über die Selektionstheorie Wasser auf die Mühle tragen?! Es wird Einem ja schwindlig, wenn man an diesen babylonischen Turnbau nur denkt!'' W. E. RITTER.

VERTEBRATE PALEONTOLOGY

Pelycosauria of North America.[1]—There are few groups of animals at the present day of greater interest to the paleontologist and evolutionist than the extinct air-breathers of the Permian; and, of the Permian vertebrates, those of America, in their abundance, variety and excellence of preservation are easily the chief. As is well known, Professor Case has, for the past ten years or more, given much intelligent attention to the Permian reptiles of America, and especially to the group which he has described in the present handsome memoir as the ''suborder'' Pelycosauria. And the writer is inclined to think that he is a little too conservative here, for he believes that the structural characters are so diverse, so widely divergent from those of the modern Sphenodon, that to include them both in one and the same order is to hinder rather than advance an intelligent taxonomy of the reptiles. Mr. Case has given in the volume a complete history of the literature of the group, a taxonomic revision, a thorough discussion of the structural characters of the pelycosaurs, and the facts of their range and distribution. He has not, rather wisely, entered very fully into the many philosophical matters that the animals suggest. He expresses the opinion, however, that the pelycosaurs represent a highly specialized and short-lived branch of the rhynchocephalian stem, and in that he will probably have the concurrence of most paleontologists. But, to the writer, this does not seem altogether certain. The group has an abundance of generalized characters in the vertebræ, pectoral and pelvic girdles, cleithra, etc., the specialization consisting, for the most part, in the extraordinary and most bizarre elongation of the vertebral spines, the teeth, etc. His reasons for the grouping he makes are chiefly to be found in the temporal region of the skull; and the writer

[1] Case, E. C. Revision of the Pelycosauria of North America. *Memoir of the Carnegie Institution of Washington*, pp. 1–176, pls. I–XXXV, 1907.

does not think he is expressing too heretical an opinion when he doubts the great importance of this region in the primary classification of the reptiles. The grouping of the reptiles into two subclasses, the Diapsida and Synapsida, based chiefly upon the temporal structure, is rejected by most students of the reptiles, and the very aberrant structure of this region in the pelycosaurs, especially the presence of a "prosquamosal" bone, rather shakes one's faith. However, we are not quarrelling with the author for not going into these doubtful discussions. He has, what is better, given us excellent material for future philosophizing in his full and lucid descriptions and many illustrations.

S. W. WILLISTON.

The Conrad Fissure.[1]—Mr. Brown has given us in this paper an excellent critical and descriptive list, well illustrated, of a very important pleistocene bone deposit, especially interesting as located in the southwest. The material, for the most part collected, and it need not be said skillfully collected by the author, is abundant, including seven species of insectivores, two of bats, nineteen of carnivores, as many of rodents, and nine of ungulates, together with several of amphibians and reptiles. Of these he describes a new twenty species and two genera, the more noteworthy of the new genera being one of a new type of saber-toothed cats. Conspicuous for their absence are remains of the large edentates and of the proboscideans, from which the author is inclined to the belief that the former, at least, were not then in existence in North America. That some of the sloths were in existence in South America at that period is more than probable, if we take into account Gryphotherium, and the same logic would exclude the proboscideans from the fauna, which is not at all probable. He also concludes that the fauna was boreal, as indeed would be indicated by the remains of musk oxen. The paper is a valuable addition to our faunal pleistocene literature.

S. W. WILLISTON.

The Ankylosauridae.[1]—Mr. Brown has given us a rather startling restoration of what he believed to be a new family of

[1] Brown, Barnum. The Conrad Fissure, A Pleistocene Bone Deposit in Northern Arkansas, with Descriptions of Two New Genera, and Twenty New Species of Mammals. *Mem. Amer. Mus. Nat. Hist.*, IX, pp. 157–208, pls. XXIV, XXV, 1908.

[1] Brown, Barnum. The Ankylosauridæ, A New Family of Dinosaurs from the Upper Cretaceous. *Bulletin of the American Museum Nat. Hist.*, X, XXIV, pp. 187–201, 1908.

armored dinosaurs from the Hell Creek Beds of Montana. The material, however, upon which he bases his restoration was scanty—too scanty to serve as a satisfactory basis for a restoration—consisting of the skull, a number of vertebræ, a somewhat problematical scapula, and a number of dermal scutes. The dangers of such attempted restorations as the present one on such imperfect material are apparent here, since Ankylosaurus is either very closely allied to or identical with Stegopelta Williston, a genus overlooked by Mr. Brown. And Stegopelta, which is represented by considerable material in the University of Chicago collections, is as closely allied as well may be with Polacanthus Hulke of England, and must go in the same family. A comparison of Nopsca's restoration of Polacanthus, which is essentially correct, save for the skull, will show the real form of Ankylosaurus, very different from that given by Mr. Brown. Stegopelta, moreover, has spines, and the body is covered in large part by small scutes, though there are also large ones, as figured by Mr. Brown; and the tail rings are correctly placed by Brown. The writer has examined the specimen in the British Museum, and is assured of the relationships. Stegopelta will shortly be more fully described and figured by Dr. Moodie.

S. W. WILLISTON.

PARASITOLOGY

The Evolution of Parasitism.—In a recent paper entitled: "The Influence of Symbiosis upon the Pathogenicity of Microorganisms (The Evolution of Parasitism)," Musgrave[1] has brought together some most important items in an extremely suggestive manner. He defines symbiosis as representing all phases of association between living organisms, beginning with commensalism, on the one hand, and including true parasitism, on the other, in which either component is influenced in nutrition, metabolism, production or in some other manner by the presence of the other. While this use of the term is distinctly new and rather at variance with the older usage of van Beneden the meaning of the author is clear. He endeavors to show that symbiotic combinations between microorganisms are responsible for uninterpreted phenomena in the etiology and pathology of disease. Furthermore, he adduces evidence to show that changes is symbiosis may produce changes in metabolism and also, as a result of this,

[1] *Philippine Jour. Sc.*, B 3: 78.

changes in the pathogenic character of parasites and in the susceptibility of hosts. The work of other authors is cited indicating the influence that surroundings have on cultures of bacteria even under experimental conditions and leading to the conclusion that the relation between nutrition, metabolism and production is far more significant than has heretofore been considered in laboratory technique. If such influences modify artificial cultures, there will surely be a much greater effect from the complex conditions surrounding mixed cultures in unknown symbiosis.

Among animal parasites nutrition, metabolism and production certainly are more complicated than with bacteria, and unless this fact is constantly in mind the whole subject of parasitism is apt to be considered along too narrow lines and our specificities to be regarded as too exacting. The question, just as with bacteria, not only involves a study of the interaction between an animal host and animal parasites, but a study of host under constantly varying conditions being acted upon by parasites influenced by an ever-changing environment. A battle, as it were, takes place between two sets of very complex influences, leading to death or disease of the host on the one hand, to destruction or commensalism on the part of the parasite on the other, or finally quite frequently to what Theobald Smith has called a condition of balanced parasitism.

Most suggestive in this direction is the experimental work which has been done with amœba. Chief among the investigators are Musgrave and Clegg, who found that the cultivation of amœba could not be accomplished satisfactorily except in the presence of other living organisms, and this symbiosis is more or less specific although its specific character may be changed both experimentally and probably also under natural conditions.

The author sums up his paper as follows:

"I am convinced that such an evolution of parasitism from an amœbic and bacterial symbiosis, in water or elsewhere in nature, through a beginning or mixed tissue and bacterial parasitism in amœbic ulcers of the colon, to a true tissue parasitism in the internal organs of the body, or even to a blood invasion itself, is a matter of frequent occurrence. The most promising field for laboratory research in the future will be the study of cause and effect, in the complex relations in which they occur in nature, of the interrelation and interaction of microorganisms with each other and in their environment of complex symbiosis and the ever-changing and multiple conditions found in hosts."

Trypanosomes.—The life history of various trypanosomes has been investigated with great care at the Runcorn Research Laboratory, Liverpool, by J. E. S. Moore and A. Breinl, with several collaborators. The results appear to be uniform and to differ markedly from those of previous work. These authors are unable to make any distinction between the so-called male, female and parthenogenetic forms of Schaudinn and hold that mere varieties in size or even in some morphological features when taken from different parts of the life cycle should not be spoken of under terms which imply conjugation when no such phenomenon takes place so far as is known. *Trypanosoma gambiense* and *T. lewisi* manifest a cyclical metamorphosis corresponding closely to alternate presence and absence of the parasites from the blood. Periods of maxima and minima alternate irregularly and not with the definite chronicity seen in the development of the malarial organisms. The coming of a minimum is accompanied by the formation of latent bodies consisting of nucleus and vesicle enclosed by a delicate covering of cytoplasm. These latent bodies lodge chiefly in the spleen and bone marrow and from them are developed later a new generation of the typical flagellate forms. Associated with the formation of the latent bodies is an interaction, which occurs at or near the maxima, between the extra-nuclear centrosome, perhaps better named the blepharoplast and the nucleus. It is inferred that the real sexual phase occurs within the transmitting insect, although other investigators look upon the rôle of the latter as purely mechanical.

In *T. equiperdum*, which is the cause of dourine, the entire life history is confined to a single animal and not complicated by transfer through an intermediate host. When inoculated in a rat the process appears identical with that outlined above, save that the round forms which occur at the period characteristic of latent bodies possess two long and delicate flagella. There is in the rat but a single maximum which is followed by the death of the host; in horses the parasites are not sufficiently numerous to permit the observer to follow the changes which take place.

H. B. W.

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